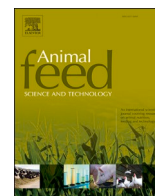




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Review article

Sericea lespedeza (*Lespedeza juncea* var. *sericea*) for sustainable small ruminant production: Feed, helminth suppressant and meat preservation capabilities

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ABSTRACT

Small ruminants significantly contribute towards livelihood, food and nutrition security for people living in semiarid low-to-middle-income countries. However, their productivity is largely constrained by feed shortages, prevalence of gastrointestinal nematodes (GIN) and postharvest meat losses. The current review explores the possibility of using sericea lespedeza (*Lespedeza juncea* var. *sericea*) as a natural helminth suppressant, feed ingredient and meat preservative for improving small ruminant health, meat production and shelf life. Sericea lespedeza has moderate contents of crude protein, fibre, minerals, vitamins, amino acids, and diverse composition of physiologically active substances such as condensed tannins, sterols and flavanols from which it derives nutritional, anti-bloat, helminth suppressant, antimicrobial and antioxidative properties. Overall, the present review demonstrates the potential of feeding sericea lespedeza to small ruminants as a sustainable means of controlling GIN and enhancing meat production and shelf life, while also reducing greenhouse gas (GHG) emissions. However, more research is required to determine optimal feeding strategies and doses for reducing GHG emissions while improving health, meat production and quality of small ruminants.

1. Introduction

Domesticated ruminants, including sheep and goats contribute significantly towards food and nutrition security, particularly for people living in semiarid regions of low-to-middle-income countries (Enahoro et al., 2019; Mlambo and Mapiye, 2015). Semiarid areas are characterised by short rainy seasons with inconsistent rainfall patterns, which makes crop farming challenging. Thus, most households in these dry areas rely on livestock farming, especially small ruminants (i.e., sheep and goats) for their maintenance (Ben Salem and Smith, 2008; Enahoro et al., 2019). As of 2018, 42 and 31 % of the world's 1.0 and 1.2 billion goats and sheep, respectively, were reared in Africa (FAO, 2019a). Apart from their significant contribution towards the economy, small ruminants can convert low-value human-inedible feed input into high-value human-edible protein output in the form of meat and milk (Ben Salem and Smith,

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2008; Enahoro et al., 2019; Salami et al., 2019). This highlights their importance as a vehicle for fostering food and nutrition security in semiarid, low-to-middle-income countries.

The productivity of small ruminants in semiarid regions is generally constrained by inconsistent supply of nutritious feed (Ben Salem and Smith, 2008; Meissner et al., 2013; Mlambo and Mapiye, 2015). Decline in productivity as a result of gastrointestinal nematode (GIN) infections is also a common constraint (Kearney et al., 2016; Ketzis et al., 2006). In addition, up to 263 million tonnes of meat are lost at post-harvest phase globally (FAO, 2019b), with significant losses occurring due to oxidative deterioration and microbial spoilage (Cunha et al., 2018; Papuc et al., 2017). Synthetically manufactured feed supplements (e.g., urea, biuret and ammonium salts; Currier et al., 2004; Löest et al., 2001; Oba and Allen, 2003), anthelmintics (e.g., benzimidazoles, macrocyclic lactones and amino-acetonitrile derivatives; Besier et al., 2016) and meat preservatives (e.g., gallates, lactates and ascorbates; Ribeiro et al., 2019) have been used to improve ruminant performance, gastrointestinal health and meat quality, respectively. However, scarcity and high costs of these synthetics, especially in resource-limited communities, and increased consumer awareness of chemical residues within animal products and the environment have limited their utilisation in small ruminants (Mazhangara et al., 2020; Cunha et al., 2018; Makkar, 2016). Moreover, some of the synthetic anthelmintics and meat preservatives are linked with increased resistance in GIN (e.g., *Haemonchus contortus*, *Trichostrongylus* and *Ostertagia* species; Zvinorova et al., 2016) and meat pathogens (e.g., *Enterococcus faecium*, *Escherichia coli* and *Staphylococcus aureus*; Aziz and Karboune, 2018; Miranda et al., 2009), respectively. Henceforth, the development of sustainable strategies which conform to the concept of 'clean, green and ethical' animal health, meat production and preservation should be prioritised (Durmic and Blache, 2012; Kearney et al., 2016; Terrill et al., 2012).

In recent times, a wide range of polyphenolic-rich invasive legumes including *Lespedeza juncea* var. *sericea*, *Lespedeza striata*, *Acacia* and *Vachellia* species have been utilised as feed, anti-bloat agents, helminth suppressants, biopreservatives and greenhouse gas (GHG) emissions reducing agents in small ruminant meat production systems (Animut et al., 2008; Idamokoro et al., 2016; Puchala et al., 2018, 2012a; Terrill et al., 2012). *Lespedeza juncea* var. *sericea* is characterised by moderate contents of crude protein (CP), fibre, minerals and vitamins (Acharya et al., 2019; Ding et al., 2006; Kim and Kim, 2010; Moore et al., 2008), and diverse composition of physiologically active compounds such as condensed tannins (CT), flavonoids and sterols (Kim and Kim, 2010; Kim et al., 2011). Owing to its moderate nutritional and high bioactive potential, the focus is now shifting from its eradication as an invasive species to utilisation as a multipurpose legume to improve animal health, meat production and quality (Terrill et al., 2012; Terrill and Mosjidis, 2017). However, adoption of *L. juncea* var. *sericea* among other legumes with multi-bioproperties worldwide is still in its infancy because most of the traditional knowledge lies in the hands of elderly smallholder farmers without rigorous scientific validation (Kearney et al., 2016; Mazhangara et al., 2020; Sanhokwe et al., 2016). The current review, therefore, appraises the nutritional and bioactive properties of *L. juncea* var. *sericea*, and demonstrates its potential as a sustainable natural feed ingredient, anti-bloat agent, helminth suppressant and meat preservative in small ruminant production.

2. Taxonomy and nomenclature

Lespedeza juncea var. *sericea* (Thunb.) Lace & Hauech (family Fabaceae/Leguminosae), also known *Lespedeza cuneata* (Dum.Cours.) G. Don is a perennial warm season shrubby legume with 14 synonyms (European and Mediterranean Plant Protection Organization [EPPO], 2019). According to The Plant List (2013), *L. juncea* var. *sericea* (Thunb.) Lace & Hauech is the accepted name of an infra-specific taxon of the species *L. juncea* (L.f.) Pers. The most common English names are Chinese bush clover, sericea and sericea

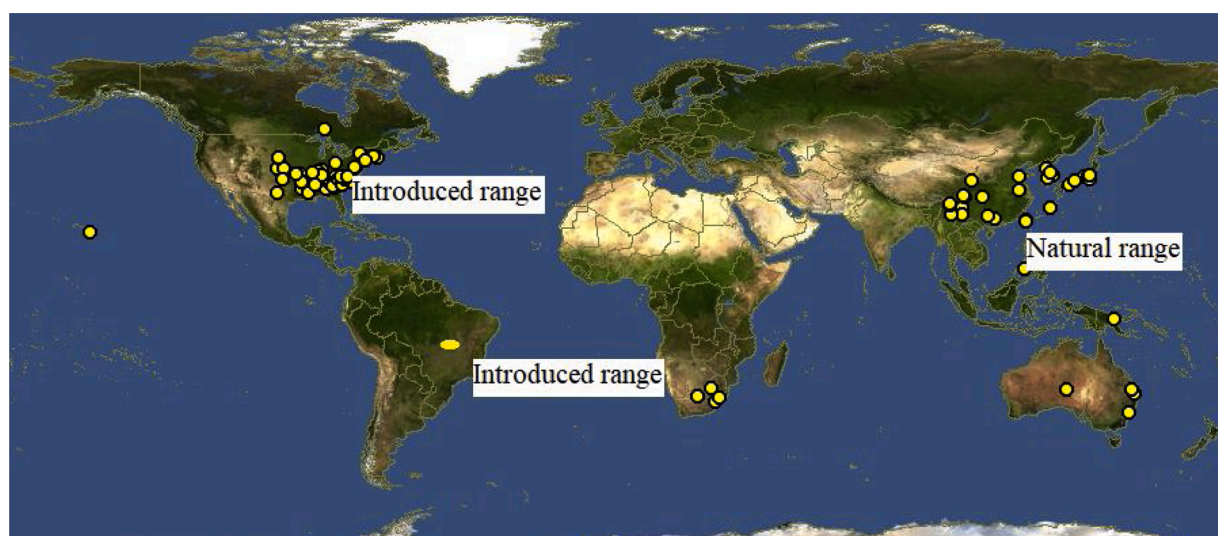


Fig. 1. Global distribution (yellow dots) map indicating the occurrence of sericea lespedeza (http://www.discoverlife.org/mp/20m?kind=Lespedeza+cuneata&guide=North_American_Invasives) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

lespedeza. *Lespedeza juncea* var. *sericea* was named “poor man’s lucerne” and later “smart man’s lucerne” owing to its ability to thrive in low quality soils without fertiliser application while bearing many animal and human beneficial functions (Fair, 2014; Terrill and Mosjidis, 2017). In this review, *L. juncea* var. *sericea* is referred to as sericea lespedeza (SL) because it is the commonly used name in the literature cited herein.

3. Ecological distribution

Sericea lespedeza has a wide global distribution and occurs mainly in Asia, North America, Oceania and southern Africa (Fig. 1), but native to Australia, China, India, Japan, and Taiwan (EPPO, 2019). The first planting of SL outside its natural habitat was in south eastern United States of America (USA) in late 19th century (EPPO, 2019; Terrill and Mosjidis, 2017). It has, however, been declared a noxious weed in various states in the USA (EPPO, 2019). To date, SL has been adapted in several other countries including Brazil, Canada, Eswatini, Mexico, and South Africa (EPPO, 2019; Fair, 2014; Mkhathshwa and Hoveland, 1991). In South Africa, it is cultivated for pasture on commercial farms, but also occurs in the wild or along roadsides in five Provinces namely Eastern Cape, Free State, Gauteng, KwaZulu-Natal and Mpumalanga (South African National Biodiversity Institute, 2016).

4. Agronomic potential of sericea lespedeza

Sericea lespedeza grows in widely variable edaphoclimatic conditions including nutrient-poor, acidic, shallow clayey and loamy soils, hence its global establishment in degraded savannah rangelands (Mikhailova et al., 2016; Mkhathshwa and Hoveland, 1991). It survives and grows well in arid to semiarid areas where average annual rainfall is below 300 mm (Mkhathshwa and Hoveland, 1991; Muir et al., 2017a, 2017b). Sericea lespedeza plants are prolific seed producers, bearing between 325–975 kg seed/ha (EPPO, 2019). Seedling germination and growth require optimal day and night temperatures of 26–30 °C and 22–26 °C, respectively, and day length of 13–15 h (Mosjidis, 1990). Their long taproot enables water extraction from deep within the soil, thereby improving vigour and survival during dry periods (Mkhathshwa and Hoveland, 1991). Additionally, the deep root system fixes nitrogen in the soil and utilises soil-bound phosphorus, which is biologically unavailable for use by other plants, thus reducing the need for external application of inorganic fertilisers (Mkhathshwa and Hoveland, 1991; Terrill and Mosjidis, 2017). Due to heavy seed production, strong seedling vigour and persistence, SL has potential to outcompete native species in some ecosystems resulting in formation of dense woody and fibrous thickets, potentially becoming invasive if underutilised (Muir et al., 2017a, 2017b).

Established SL provides heavy shading for shorter plants, subsequently restricting the amount of light reaching these competing plants (Brandon et al., 2004; Ohlenbusch et al., 2007). In addition, SL roots exude allelopathic chemicals which reduce germination, emergence, radicle and coleoptile length, and above-ground biomass of some pasture grasses including bermudagrass, bahiagrass, ryegrass and tall fescue among others (Dudley and Fick, 2003; Kalburtji and Mosjidis, 1993; Ohlenbusch et al., 2007). It has been suggested that allelopathic chemicals from SL reduce the performance of native grass species by up to 60 % (Dudley and Fick, 2003), thus threatening complete takeover if not controlled. Sericea lespedeza invasions may lead to loss of habitat heterogeneity for insects and small mammalian species (Howard, 2013). Increasing the vegetative cover of SL favours the development of communities composed of relatively few, but individually abundant small mammalian species (Howard, 2013). This underscores the importance of properly managing SL pastures to preserve naturally occurring flora and fauna, and maintain healthy ecosystems. Ohlenbusch et al. (2007) noted that SL could grow in ditches, fence rows, or pastures without invading adjacent well-managed rangeland and pastures, thus highlighting the effectiveness of proper pasture management as a control measure against invasive spread of SL.

5. Uses of sericea lespedeza

Traditionally, roots and aerial parts of SL were used in Asian ethnomedicine for treatment of asthma, abscesses, some cancers and protection of liver and kidney function in humans (Kim and Kim, 2010; Kim et al., 2011). Despite being introduced for soil conservation (i.e., prevention of soil erosion, reclamation of minefields and roadsides) in USA, it was also used as forage and for prophylaxis of bloat and helminths in livestock (Terrill et al., 2012; Terrill and Mosjidis, 2017). Sericea lespedeza may be used in rotational grazing systems in an integrated anthelmintic control plan (Burke et al., 2012a; Terrill et al., 2012). Current research demonstrates that fodder can be harvested up to 11 tonnes/ha and processed into various forms (i.e., hay, pellets, leaf meals and/or silage) for supplementation during periods of low feed availability (Acharya et al., 2019; Kronberg et al., 2018; Singh et al., 2019; Terrill and Mosjidis, 2017). Feeding SL forage enhances small ruminant milk quality (Min et al., 2005, 2008), but its potential for modulating meat production and quality has not been fully explored. Due to increasing requirements for alternative feed resources with nutritional, helminth suppressant and biopreservative properties, the demand for SL-derived products is growing fast (Terrill and Mosjidis, 2017).

6. Nutrient and bioactive profile of sericea lespedeza

6.1. Chemical composition

Overall, the proximate and amino acid compositions of SL forage show that its CP content is above the minimum range required for normal rumen function and maintenance, and within the range required for production (i.e., growth, pregnancy and lactation) of small ruminants (Table 1). The metabolisable energy content is slightly above acceptable ranges required for growing and finishing small ruminants, while the neutral detergent fibre (NDF) and acid detergent fibre (ADF) contents are above recommended minimum

requirements for normal rumen function. Overall, the range for proximate composition of SL, though influenced by origin, environmental conditions, seasons, varieties, maturity, plant tissues and harvest frequencies (Acharya et al., 2019; Muir et al., 2017a, 2017b), is comparable to that of Lucerne and other legumes (Lee, 2018; Puchala et al., 2012a), highlighting its potential as an alternative feed resource for small ruminants in tropical regions. However, the large variation observed requires that chemical characterisation of SL be completed before inclusion into livestock diets.

Concentrations of methionine, the most limiting amino acid for small ruminants, falls short of the estimated minimum requirements for maintenance and growth of small ruminants (Table 1). Similarly, the concentrations of other essential amino acids in SL were lower than the minimum required for growing small ruminants (Table 1). Therefore, utility of SL in diets requires amino acid supplementation or co-feeding with other protein sources. Except for sodium and selenium, all macro- and micro-mineral contents, respectively, are above recommended levels for growing small ruminants (Table 2). Deficiencies of either sodium or selenium or both may compromise immune function, reproductive physiology and weight gain (NRC, 2007), hence animals should be supplemented with these minerals when SL is fed as a sole diet. The iron content of SL hay is greater than that of Lucerne hay whereas manganese, zinc and copper concentrations are lower (Table 2).

6.2. Polyphenolic compounds and their *in vitro* bioactivity

The phytochemical composition of SL is presented in Table 3. The relatively high mean concentration (above 80 g/kg DM) of CT in SL may reduce feed intake and nutrient digestibility (Min and Solaiman, 2018; Mueller-Harvey et al., 2019). However, the CT fraction of SL is predominantly prodelphinidin, with only a small proportion of procyanidins (Table 3). The high content of prodelphinidin CT and its monomers (gallocatechin, epigallocatechin and their galloyl derivatives) contribute to its high affinity for proteins including proline- and hydroxyproline-rich structures (Kommuru et al., 2015, 2014; Mechineni et al., 2014). In terms of the CT content in different plant parts, the leaf generally has greater quantity than the stem (Mechineni et al., 2014; Donnelly and Anthony, 1973; Petersen et al., 1991). The mean degree of polymerization (mDP) of CT was 42 for leaves compared to 18 for stems. Similarly, the *cis*-flavanol proportion was greater in the leaves (91 %) compared to stems (84 %) (Mechineni et al., 2014). There is also great variability in total, protein-bound and fibre-bound CT concentrations in SL (Table 3), which is mostly due to differences in edaphoclimatic conditions, variety, maturity and harvest frequency (Muir et al., 2017a, 2017b, 2014).

Phytochemical screening of SL aerial parts revealed presence of C-glycosylflavones (desmodin, homoanonivernith, isoorientin, lucenin-2 and vicenin-2), O-glycosylflavonols (avicularin, hirsutrin, hyperin, juglanin and trifolin), aglycones (kaempferol and quercetin) and sterols (β -sitosterol) (Kim and Kim, 2010; Kim et al., 2011), among others (Table 3), but little is known about their concentrations, and merits further research. This is particularly important because some O-glycosylflavonols and C-glycosylflavones such as avicularin and isovitexin, respectively, have shown promising anti-inflammatory and antioxidant properties *in vitro* (Kim et al., 2011; Lee et al., 2019).

The antioxidant activity of polyphenols is mediated through their redox properties, which allow them to act as reducing agents, hydrogen donors, pro-oxidant metal ion chelators and/or singlet-oxygen quenchers (Apak et al., 2016; Chikwanha et al., 2019a; Kim and Kim, 2010). Overall, aerial parts of SL demonstrated antioxidant properties through the use of hydroxyl (OH) and 2,

Table 1
Proximate and amino acid composition of sericea lespedeza forage.

Chemical composition (g/kg DM)	Min	Mean *	Max	Min. requirements #
Organic matter	93.8	94.7	96.0	–
Crude protein	94.0	148	212	60 – 170
Neutral detergent fibre	340	435	603	250 – 330
Acid detergent fibre	247	323	489	170 – 210
Lignin (sa)	54.0	92.3	231	<40
Ash	70.0	103	120	–
Ether extract	12.0	16.3	20.0	<80
Metabolisable energy (MJ/kg)	17.6	19.1	20.2	6 – 16
<i>In vitro</i> dry matter digestibility	267	435	741	–
Amino acids (g/kg DM)				
Arginine	1.43	4.42	7.40	56.5 **
Cysteine	–	1.60	–	–
Histidine	0.78	1.84	2.90	26.9
Isoleucine	1.15	3.38	5.60	29.4
Leucine	1.78	6.69	11.6	78.6
Lysine	2.93	6.07	9.20	68.3
Methionine	0.56	1.38	2.20	18.3
Phenylalanine	1.13	4.17	7.20	30.4
Threonine	1.31	3.71	6.10	55.5
Valine	1.33	1.33	–	48.6

* Means are averages of values obtained from literature.

Ranges for the minimum requirements for maintenance and growth according to NRC (2007).

** Composition of minimum requirements expressed as g/kg CP according to Ferreira (2004).

Sources: (Ding et al., 2006; Gujja et al., 2013; Kommuru et al., 2014; Muir et al., 2017a, 2014; Powell et al., 2003; Puchala et al., 2018, 2012a)

Table 2
Mineral and vitamin composition of sericea lespedeza forage.

Mineral	Min	Mean *	Max	Min. requirements #
Macro (g/kg DM)				
Calcium	5.90	10	17.9	1.4 – 7
Phosphorus	0.40	1.1	1.90	0.9 – 3
Magnesium	1.10	1.7	2.40	0.9 – 1.2
Potassium	3.00	6.1	10.2	5
Sodium	0.14	0.4	0.26	0.7 – 1.0
Sulphur	0.80	1.7	3.30	2.0
Micro (mg/kg DM)				
Iron	164	240	360	30 – 40
Zinc	20.0	26	37.0	9 – 33
Manganese	74.0	168	254	20 – 40
Copper	5.00	6.8	8.40	4 – 14
Cobalt	0.26	0.3	0.37	0.1 – 0.2
Molybdenum	0.19	0.4	0.56	0.5
Selenium	0.07	0.08	0.08	0.05 – 0.3

* Means are averages of values obtained from literature.

Ranges for the minimum requirements for maintenance and growth according to NRC (2007).

Sources: (Acharya et al., 2016; Ding et al., 2006; Karalić et al., 2007; Mikhailova et al., 2016)

Table 3
Phytochemical composition of sericea lespedeza forage.

Tannin fraction (g/kg DM) ¹	Min	Mean *	Max
Total condensed tannins	33.0	81.9	224
Protein bound condensed tannins	18.0	24.2	47.0
Fibre bound condensed tannins	1.00	4.10	5.00
Extractable condensed tannins	39.0	48.4	60.0
Prodelphinidins	936	953	980
Procyanidins	20.0	49.0	60.0
Flavonoids fraction (mg/kg DM) ²			
Avicularin	0.10	0.36	1.15
Isovitexin	0.35	0.64	1.45
Quercetin	0.51	1.13	1.76
Juglanin	0.14	0.26	0.37
Quercitrin	0.17	0.26	0.36
Kaempferol	0.14	0.34	0.54
Vitamins (mg/kg DM) ³			
Vitamin E	–	330	–
Vitamin B ₅	–	90.0	–
Vitamin B ₁	–	78.0	–
Vitamin B ₆	–	17.0	–

* Means are averages of values obtained from literature.

Sources: ¹ (Gujja et al., 2013; Kommuru et al., 2014; Muir et al., 2017a, 2017b, 2014; Powell et al., 2003; Puchala et al., 2018, 2012a; Terrill et al., 2007); ² (Lee et al., 2019; Seong et al., 2017); ³ (Ding et al., 2006)

2-diphenyl-1-picrylhydrazyl (DPPH) radical scavenging assays (Kim and Kim, 2010; Lee et al., 2019). Lee et al. (2019) found that the OH radical scavenging capabilities of avicularin and isovitexin isolated from SL were 88 and 91 %, respectively, whereas their DPPH radical scavenging capabilities were 71 and 58 %, respectively, at a concentration of 100 µg/mL. In addition, Kim and Kim (2010) observed that the DPPH radical scavenging activity of SL extracts was stronger (95 %) than butylated hydroxytoluene (40 %), but comparable to that of vitamin E (α-tocopherol; 97 %). Although antioxidant activity of polyphenols could be 50 times greater than α-tocopherol (Uchida et al., 1987), both these antioxidants could exert additive, synergistic or antagonistic influence on overall antioxidant capacity of SL (Apak et al., 2016; Chikwanha et al., 2019a).

Although the total concentration of vitamin E in SL (Table 3) is lower than Lucerne (600 mg/kg DM; Baldi et al., 2019), it exceeds both the target physiological requirements of growing lambs (15–40 mg/kg diet) and concentration (250–290 mg/kg diet) required to exert antioxidant properties in muscle post-mortem (Álvarez et al., 2008; NRC, 2007). For instance, Álvarez et al. (2008) indicated that a target dietary vitamin E supplementation of 287 mg/kg feed, corresponds with a concentration of 2.26 mg α-tocopherol/kg meat which can reduce pigment oxidation by more than 30 % during 28 days of storage in modified atmosphere packaging. This suggests that SL could be an excellent source of vitamin E for small ruminants. The concentration of the most biologically active form of vitamin E, α-tocopherol (Baldi et al., 2019; Bellés et al., 2019) in SL is, however, not known and merits investigation. To the authors' knowledge, there are limited studies on the antimicrobial properties of dietary SL on small ruminant shelf-displayed meat and this warrants further research. Overall, the presence of bioactive compounds in SL justifies its use in ethnoveterinary medicine and

Table 4
Summarised effects of feeding sericea lespedeza (SL) on feed intake, nutrient digestibility, internal parasites and growth performance.

*Animal class	Treatment	Main findings	Reference
Does and kids	Naturally infected grazing SL (45–155 g CT ¹ /kg DM) for 12 weeks	Reduced FEC ² (85%) Inhibited establishment of incoming larvae (70 %) Reduced adult worm counts of <i>Haemonchus contortus</i> (89%), <i>Teladorsagia circumcincta</i> (100%) and <i>Trichostrongylus colubriformis</i> (50%) Improved immune function of does ADG ³ of kids declined by 10%	(Min et al., 2005)
Lambs	Natural and experimental <i>H. contortus</i> treatment fed SL hay <i>ad libitum</i> (224 g CT/kg DM) supplemented with 16% CP lamb finishing ration for 7 weeks	Reduced FEC (67–98%) Inhibited establishment of incoming larvae (26 %) Reduced worm counts (67 %)	(Lange et al., 2006)
Kids	Naturally infested kids fed ground or pelleted SL (75 % of DM intake; 65 g CT/kg DM) hay for 5 weeks	Pelleted SL reduced FEC more (70 %) than ground SL (54 %) PCV ⁴ was greater for pelleted compared to ground SL (30 % vs. 23 %) Pelleting SL increased effectiveness (75 %) against adult worms compared to ground SL (38 %)	(Terrill et al., 2007)
Kids*	Naturally infested yearling bucks fed increasing levels of ground SL hay (i.e., 25, 50, 75 %) for 6 weeks	Dose and time dependent reduction of FEC and PCV After 3 weeks FEC declined (45, 66, and 75 %, respectively) compared to (66, 82 and 92 %, respectively) after 6 weeks PCV was higher (28 %) for 75 % inclusion level Effective doses were 50 % and 75 %	(Dykes et al., 2006)
Kids	Naturally infected and dewormed subjected to 75 % bermudagrass or SL (65 g CT/kg DM) hay-based diets for 14 weeks	SL increased feed intake by 34 % regardless of infection status SL improved ADG (27 %) and final live weight (10 %) regardless of infection status SL reduced FEC (80–90%) SL improved PCV (32 %) for the SL group	(Moore et al., 2008)
Kids	Naturally infested confined weaned kids fed 75 % SL (224 g CT/kg DM) basal diet for 11 weeks	FEC declined by 80%–90% Reduced faecal larva by 58 % Reduced adult male and female worm counts by 61 % and 76 %, respectively	(Shaik et al., 2006)
Wether goats	Fed fresh SL forage (199 g CT/kg DM) or hay (153 g CT/kg DM) at 1.3 times the metabolizable energy requirement for maintenance	Fresh SL forage improved DM and OM intake by 13 and 20 %, respectively, but reduced N intake by 22 % when compared to Lucerne Fresh SL forage SL reduced DM, OM and N digestibility by 18, 20 and 43 %, respectively, when compared to Lucerne SL hay improved DM and OM intake by 14 and 16 %, but did not influence N intake when compared to Lucerne SL hay reduced DM, OM and N digestibility by 19, 12 and 24 %, respectively when compared to Lucerne Fresh SL forage reduced methane emission by 37 % whereas the hay reduced by 40 % when compared to Lucerne Fresh SL forage and hay did not influence ruminal bacteria but reduced ciliate protozoa by 53 and 54 %, respectively Fresh SL forage had no effect on ruminal ammonia N, but the hay reduced it by 64 %	(Puchala et al., 2012a)
Wether goats	Fed fresh SL (153 g CT/kg DM) at 1.3 times the metabolizable energy requirement for maintenance every day (1SL), other day (2SL), fourth day (4SL), and eighth day (8SL)	DM intake was not affected by frequency of feeding SL Daily ruminal methane emissions increased at a decreasing rate as frequency of SL feeding decreased (6.3, 7.4, 10.5, 12.0 g/d for 1SL, 2SL, 4SL, and 8SL, respectively) Carryover effects of feeding SL on ruminal methane emissions Increased protozoal counts at a declining rate with decreasing frequency of feeding SL (6.5, 10.4, 18.4, 20.5 × 105/mL for 1SL, 2SL, 4SL, and 8SL, respectively).	(Puchala et al., 2012b)
Lambs*	Naturally infected grazing SL pasture for 5 weeks	Reduced FEC up to 87 % Increased PCV from 27 to 30 % Similar ADG	(Burke et al., 2012a)
Lambs and kids*	Naturally infected lambs and kids grazing SL pasture for 8 and 14 weeks, respectively	Reduced FEC in lambs when <i>H. contortus</i> was the predominant nematode Reduced mean number of deworming required per lamb by up to 71 % No influence on FEC in kids when <i>Trichostrongylus</i> spp. were the predominant nematode Initially similar ADG which decline on day 56 in both lambs and kids	(Burke et al., 2012b)
Lambs and kids	Grazing, supplemented with 900 g SL leaf meal pellets (39–40 g/kg CT) for 8–16 weeks	ADG of lambs between day 0 and 56 was either similar, tended to be greater or greater for SL depending on year and location ADG of kids between day 0 and 56 was lower for SL	(Burke et al., 2014)

(continued on next page)

Table 4 (continued)

*Animal class	Treatment	Main findings	Reference
Kids*	Kids of different body condition scores (i.e., 2, 3, 4) fed Lucerne, SL and SL plus PEG ⁵ for 5 weeks	Lower ADG in SL fed lambs and kids were recorded during the latter growth phase SL plus PEG improved DM intake by 14 % compared to other treatments Average daily gain declined with increasing body condition scores (52, 46, -32 g/day, respectively)	(de Oliveira et al., 2017)
Wether sheep	Fed SL in pellets in increasing proportions of the diets (i.e., 10, 20, 40 %; 18, 36, 72 g CT/kg DM) for 12 weeks	No differences in DM intake Reduced DM digestibility by 6, 7.5 and 9 %, respectively Decreased NDF ⁶ digestibility by 21, 33 and 66 %, respectively Reduced ADF ⁷ digestibility by 27, 46 and 93 %, respectively Decreased N digestibility by 7, 13 and 29 %, respectively	(Kronberg et al., 2018)
Kids	Fed SL pellets in increasing proportions of the diets (i.e., 10, 20, 30 %; 7, 15, 22 g CT/kg DM) for 9 weeks	Increased DM intake by 2, 11 and 25 %, respectively ADG was similar for 30 % SL and control (30 % Lucerne) and then declined with reduced proportion of SL by 26 and 41 %, respectively Body fat thickness declined by 0, 22 and 30 %, respectively	(Solaiman et al., 2010)
Intact kids	Grazing on pure bermudagrass, SL or mixed pasture of bermudagrass and SL supplemented with commercial feed pellets	Diet had no influence on microbial status of ruminal contents and faeces	(Mechineni et al., 2020)
Kids	Grazing and growing male kids supplemented with commercial pellets, 75 and 95 % SL (0, 35 and 31 g CT/kg DM, respectively) leaf meal pellets for 11 weeks	Similar FEC decline for 75 and 95 % SL treatments (84–95%) 95% SL pellets reduced adult worm counts of <i>H. contortus</i> (93 %) and <i>T. circumcincta</i> (47 %), while only male <i>H. contortus</i> were lower (48 %) in 75 % SL compared with control Increased PCV from 22 to 30% Reduced ADG by 25 and 48 % for the 75 and 95 % SL treatments, respectively	(Gujja et al., 2013)
Kids	Experimentally infected supplemented with 75 % SL (57 g CT/kg DM) leaf meal pellets for 3 weeks	Reduced FEC (82 %) No differences in PCV with values ranging from 26 to 37% Did not influence adult worm counts of <i>H. contortus</i> , <i>T. circumcincta</i> and <i>T. colubriformis</i> Visible constricted folds and damaged cuticular surfaces of <i>H. contortus</i> worms	(Kommuru et al., 2015)
Kids	Early weaners fed 90 % SL (125 g CT/kg DM) leaf meal pellets for 3 weeks	Reduced <i>Eimeria</i> oocysts and eggs up to 79 and 97 %, respectively Reduced signs of coccidiosis, i.e., diarrhoea up to 60 %	(Kommuru et al., 2014)

¹ CT: Condensed tannins.

² FEC: Faecal egg counts.

³ ADG: Average daily gain.

⁴ PCV: Packed cell volume.

⁵ PEG: Polyethylene glycol (tannin-binding agent).

⁶ NDF: Neutral detergent fibre.

⁷ ADF: Acid detergent fibre.

* Animal class: Indicates that condensed tannin concentration was not reported.

highlights its potential for improving growth, immunity and antioxidant capacity of small ruminants.

7. Effects of feeding sericea lespedeza on small ruminant performance

7.1. Effects on feed intake

Goats tend to have greater SL DM intake than sheep (Table 4). This could be because goats have more preference and tolerance for tannin-containing (45–100 g CT/kg DM) diets compared to sheep (20–50 g CT/kg DM; Min and Solaiman, 2018; Vasta et al., 2019) whose DM intake decreases with increasing dietary CT. Puchala et al. (2005) showed higher DM intake by goats fed SL (177 g CT/kg DM) compared to those fed crabgrass. In agreement, Turner et al. (2005) observed that DM intake of SL hay in goats was greater than that of Lucerne hay and increased with time on trial for SL but declined for the latter. Conversely, reduced feed intake by sheep as CT levels increased from 31 to 181 g CT/kg DM in SL hay notwithstanding other factors (Terrill et al., 1989) may indicate the role of its CT in reducing sheep DM intake compared to goats (Min and Solaiman, 2018).

The astringency of CT reduces palatability and nutrient digestibility, which may depress voluntary feed intake (Min and Solaiman, 2018; Mueller-Harvey et al., 2019). Physiologically, not only do goats secrete more proline-rich saliva, which reduces astringency of CT, they also have greater rumen digestion rate and capacity (0.23 vs. 0.14 L/kg BW) resulting in increased rumen fill of DM (25.8 vs. 15.7 g/kg BW), thus allowing them to increase voluntary feed intake (Alam et al., 1985; Min and Solaiman, 2018; Watson and Norton, 1982). However, following continuous feeding, sheep may acquire a learned behaviour to feed on SL when grazing in mixed pastures (Burke et al., 2012b), consequently increasing their voluntary intake of SL following an adaptation period. Feed intake of sheep fed 75

% SL leaf meal in the diet was observed to be lower during the first 2 weeks but increased to approximately 95 % or greater thereafter to match lower inclusion levels and control diet (Burke et al., 2011). Lowering inclusion levels of SL through co-feeding with other ingredients low in CT (dilution technique) may enhance DM intake of sheep (Kronberg et al., 2018; Moore et al., 2008; Solaiman et al., 2010), potentially because co-feeding reduces the concentration of CT contained in the diet. Other simple techniques used to improve SL DM intake include sun-drying and pelleting apparently because the heat produced during drying and pelleting reduces the solubility and amount of extractable CT by up to 57 % (Terrill et al., 1990, 1989). Several studies reported increased intake of SL when it was offered as hay or pellets (Table 4). Moore et al. (2008) noted that feeding SL hay (65 g CT/kg DM) to goats either infected or non-infected with GIN at 75 % of the diet as fed increased feed intake by approximately 34 % regardless of infection status. On the other hand, Solaiman et al. (2010) found that inclusion of 10, 20 and 30 % SL (7, 15 and 22 g CT/kg DM, respectively) in pelleted diets improved DM intake of finisher lambs by 2, 11 and 25 %, respectively. Although dietary CT increased with increasing SL levels, greater feed intake observed in these studies (Moore et al., 2008; Solaiman et al., 2010), could be attributed the fact that the level of CT remained below 80 g CT/kg DM, a level tolerated by small ruminants depending on forage species (Min and Hart, 2003; Mueller-Harvey, 2006). Despite this progress being made in improving SL intake by small ruminants, the optimum feeding form and inclusion level of SL as a functional feed should still be established.

7.2. Effects on nutrient digestibility

In previous studies (Petersen et al., 1991; Powell et al., 2003), early varieties of SL contained higher levels of fibre and CT, which contributed towards reduced DM digestibility (Table 1). Due to continued demand for its utility, new and improved varieties of SL including AU Lotan and AU Grazer, were developed (Terrill and Mosjidis, 2017). Their high *in vitro* DM digestibility values (670–740 g/kg DM) are above those of commonly used forage legumes, making SL an important source of nutrients for small ruminants (Puchala et al., 2012a, 2012b).

Currently, *in vivo* studies do not show a clear relationship between dietary SL and nutrient digestibility (Table 4). Puchala et al. (2018) observed that inclusion of pelleted SL forage (64 g CT/kg DM) in diets of mature goats did not influence total tract digestibility of organic matter (OM), DM and fibre, but reduced nitrogen digestibility. Contrary to this, Puchala et al. (2012a) reported that feeding SL as fresh forage (199 g CT/kg DM) or hay (153 g CT/kg DM) with or without polyethylene glycol (PEG) reduced the digestibility of OM and DM, but addition of PEG improved N digestibility up to 30 % (Table 4). Polyethylene glycol is a polymer that effectively binds to CT, thereby reducing its biological activity (Mueller-Harvey, 2006; Priolo et al., 2005). The influence of PEG on N digestibility could have occurred through prevention of incomplete release of proteins initially bound to CT in the rumen or through decreased post-ruminal rebinding of CT to proteins, or both (Min et al., 2003; Mueller-Harvey, 2006; Puchala et al., 2012a). As with goats, Kronberg et al. (2018) reported linear decline of apparent digestibility of DM, fibre and nitrogen in mature sheep fed increasing proportions of SL pelleted diets (0–72 g CT/kg DM). Reduction in digestibility measures could be due to synergistic effects of high fibre concentrations (Table 1) and CT (Table 3). Lignin and CT form crosslinkages with numerous types of substances including polysaccharides, proteins, nucleic acids and minerals thereby acting as physical barriers to microbial enzymes reaching their target substances (Harper and McNeill, 2015; Min and Solaiman, 2018). Additionally, condensed tannin-protein complexes slow ruminal fermentation rate by inhibiting ruminal proteolytic microbe activity, subsequently limiting nutrient degradation (Patra and Saxena, 2011).

Low to moderate CT (20–80 g CT/kg DM; Mueller-Harvey et al., 2019; Patra and Saxena, 2011) either had neutral effects on nutrient digestibility when fed in combination with low to moderate levels of NDF (75–350 g/kg DM) (Harper and McNeill, 2015). At moderate levels, tannin-protein complexes dissociate at pH < 3.5 in the abomasum, thus increasing influx of proteins reaching the duodenum for subsequent digestion. Resultant amino acids are then absorbed in the ileum to the bloodstream and deposited into tissues resulting in improved weight gains (Mueller-Harvey et al., 2019; Patra and Saxena, 2011). However, there is no certainty about optimum inclusion level of SL in small ruminant diets to ensure optimal nutrient utilisation and animal performance, thus warrant research.

7.3. Effects on growth performance

Current research shows that goats grazing or fed other forms (i.e., hay or pellets) of SL generally had comparable or greater average daily gains (ADG) than goats fed control diets (Table 4). Few studies (Lee et al., 2012; Moore et al., 2008) have demonstrated that goats receiving higher dietary inclusion levels of SL hay (65 g CT/kg DM) up to 75 % of total diet, as fed basis had greater ADG and final weights compared to either lower inclusion levels or bermudagrass hay. Solaiman et al. (2010) also observed that complete substitution of Lucerne hay with SL hay (up to 30 % as fed; 20 g CT/kg DM) in total mixed pelleted diets improved ADG of goats. From these studies (Lee et al., 2012; Moore et al., 2008; Solaiman et al., 2010), goats receiving between 30 and 75 % of diet as SL had greater feed intake, which may have positively influenced nutrient utilisation and consequently, growth performance. More recently, de Oliveira et al. (2017) indicated that feeding whole SL pellets with or without PEG induced compensatory growth of goats.

Sheep may be more sensitive to increasing levels of CT from 45 to 100 g CT/kg DM in diets as growth can suffer due to reduced DM intake, DM digestibility and protein N digestion (Min and Solaiman, 2018). Kronberg et al. (2018) noted that increasing the proportion of dietary SL (10, 20, 40 % as fed; 18, 36, 72 g CT/kg DM) linearly reduced DM intake, nutrient digestibility, nitrogen intake and retention, which decreased ADG of lambs (Table 4). However, as with goats, Burke et al. (2014, 2012b) demonstrated that growth rate can initially be good in sheep consuming SL but slows over time. For instance, growth rate was greater for lambs supplemented with 900 g of SL leaf meal pellets up until day 56 before it started to decline (Burke et al., 2014), while the growth rate of lambs grazing pure

stand SL pasture declined after only 28 days (Burke et al., 2012b). Prolonged feeding with SL was observed to reduce serum and liver concentrations of trace minerals associated with metalloproteins (i.e., molybdenum, zinc, copper, selenium and cobalt), which probably caused depressed lamb weight gains (Acharya et al., 2016). Acharya et al. (2016) also observed more molybdenum in faeces of lambs fed SL diets. In this regard, reductions in weight gains may be associated with high CT concentration in the diet, which may have complexed with minerals making them biologically unavailable for absorption by the animal (Freeland et al., 1985; Scharenberg et al., 2007).

7.4. Effects on bloat

Sericea lespedeza has long been linked with reduced incidences of frothy bloat in ruminants (Dykes et al., 2006; Gujja et al., 2013; Terrill et al., 2012). Frothy bloat occurs as a result of rapid ruminal fermentation of soluble protein resulting in the formation of an extracellular mucopolysaccharide complex known as biofilm which traps fermentation gases, ultimately interrupting eructation patterns (Pitta et al., 2016; Wang et al., 2012). The mechanism of action of SL on frothy bloat prevention could rely on the concentration above 50 g CT/kg DM and ability of CT to precipitate protein during mastication and rumination, reduce solubility of dietary protein in the rumen, inhibiting microbial activity and decreasing the production of biofilm (Mueller-Harvey et al., 2019; Patra and Saxena, 2011; Wang et al., 2012). However, the direct mechanism of SL bioactive compounds as anti-bloat agent has not been clearly defined and is an area of further research.

7.5. Effects on methane and nitrogen emissions

Dietary polyphenols, particularly CT, from SL have received attention for their potential to inhibit methane production capacity of goats (Puchala et al., 2018, 2012a, 2012b). In these studies, feeding goats with SL reduced ruminal methane emissions by 29–52% compared to goats fed grass and grains. The mechanism of action of SL was mainly linked to the direct role of CT in reducing populations, growth and activity of methanogenic bacteria (i.e., *Methanomicrobium* and *Methanobrevibacter*) (Puchala et al., 2018, 2012a, 2012b). Alternatively, CT suppress growth and activity of fibrolytic bacteria (i.e., *Bacteroidetes*, *Eubacterium* and *Ruminococcus*) and protozoa whose role in methanogenesis lies in their ability to depress the concentration of ruminal hydrogen, which leads to reduced availability of substrates required for methane production (Puchala et al., 2018; Vasta et al., 2019).

It has been suggested that continuous feeding with CT-rich diets might modify the ruminal microbiome, or induce secretion of exopolysaccharides (i.e., glycoproteins) by some bacteria which form a protective layer around bacterial cells, thereby lessening the effectiveness CT on suppressing methane production (Bodas et al., 2012; Patra and Saxena, 2011). Puchala et al. (2018) demonstrated that this does not seem to happen in goats fed SL as their study found that the immediate effects of SL on ruminal methane emissions were maintained for 19 weeks. Although this indicates that SL could potentially be utilised to control methane emissions in the long term, there is a possible trade-off with growth performance (Burke et al., 2014, 2012b). In addition to the role of ruminal microbes, the extent of ruminal methane emission suppression is dependent on total and digestible dry matter intake (DMI). For example, Puchala et al. (2005) noted that “the degree to which methane emission was less for SL compared with crabgrass/tall fescue on an absolute basis (i.e., 30 %) became much greater when expressed relative to intake of total (57 %) and digestible DMI (50 %)”. Similarly, ruminal methane emissions relative to intake of DM and OM increased linearly with decreasing frequency (intervals of 1, 2, 4 and 8 days) of feeding fresh SL to goats (Puchala et al., 2012b). However, there were carryover effects of feeding SL on ruminal methane emissions. For example, goats fed SL on 8-day intervals did not reach maximum methane emissions until 4–5 days after feeding on SL (Puchala et al., 2012b).

With regards to nitrogen emissions, Kronberg et al. (2018) demonstrated that increasing dietary proportions of SL linearly reduced the amount of nitrogen in urine as urea up to 27 %, whereas the concentration of nitrogen excreted in faeces increased linearly up to 68 %. This could be attributed to the role of CT in depressing the rate and extent of microbial protein degradation in the rumen, thereby reducing surplus ammonia, which would be absorbed from the rumen and excreted as urine urea nitrogen (Patra and Saxena, 2011). Goats feeding on SL forage for 6 weeks had 63 % lower ruminal ammonia concentration compared to goats fed a mixture of crabgrass and tall fescue (Puchala et al., 2005). Shifting urinary to faecal nitrogen excretion is considered sustainable and could reduce nitrogen losses on farms by up to 25 %, which could reduce costs associated with nitrogen fertilisers in crop-livestock integrated systems (Hristov et al., 2019; Mueller-Harvey et al., 2019; Patra and Saxena, 2011). In addition, faecal nitrogen is less volatile compared to urine urea nitrogen, which is rapidly hydrolysed and nitrified to ammonia and nitrate, respectively, and the latter could leach into groundwater resulting in water pollution (Hristov et al., 2019; Mueller-Harvey et al., 2019; Patra and Saxena, 2011). Overall, dietary inclusion of SL may provide environmental benefits by facilitating excretion of nitrogen in faeces rather than urine, thereby reducing loss of harmful compounds to the environment.

7.6. Effects on gastrointestinal nematodes

A summary of the influence of SL on GIN is shown in Table 4. Although various GIN species are common in small ruminants, *Haemonchus contortus*, a blood-sucking nematode, is well known for its devastating effects on health, production and farm economics (Acevedo-Ramírez et al., 2019; Kearney et al., 2016; Ketzis et al., 2006). Adult *H. contortus* have an average daily consumption of up to 0.05 mL of blood per worm (Altaif and Dargie, 1978), thus daily blood losses ranging from 150–250 mL can occur in sheep carrying worm burdens ranging from 3 000–5 000 (Altaif and Dargie, 1978; Rowe et al., 1988). Globally, intensive use of synthetic anthelmintics is losing viability due to increased development of resistance among *H. contortus* populations hence it is important to find

alternative natural anthelmintics that are less prone to resistance (Acevedo-Ramírez et al., 2019; Barone et al., 2018; Castañeda-Ramírez et al., 2019).

While grazing SL is effective in controlling GIN in sheep and goats (Burke et al., 2012b; Mechineni et al., 2014; Min et al., 2004), converting the forage to hay and pellets offers more flexibility for storage, transportation and availability when needed most (Lange et al., 2006; Shaik et al., 2006; Terrill and Mosjidis, 2017). However, the processes of drying and pelletising SL may change the amount and/or structure of CT (Kommuru et al., 2014; Mechineni et al., 2014; Terrill et al., 1989). Although this may be expected to change the biological activity of SL, studies to date have shown that drying and pelletising does not negatively influence the helminth suppressant efficacy of SL (Gujja et al., 2013; Terrill et al., 2007, 2012; Terrill and Mosjidis, 2017). Feeding SL hay and pellets resulted in improved anti-nematode responses of small ruminants against *H. contortus*, *T. colubriformis*, *Teladorsagia circumcincta* and *Eimeria* species, although its effectiveness was dose and time dependent (Table 4). Responses of nematodes to fresh SL also appear to be influenced by animal species. For instance, reductions in faecal egg counts (FEC) were observed in kids and does within the first week of grazing SL pastures (Min et al., 2005; Terrill et al., 2012). Although Lange et al. (2006) reported an immediate reduction in lamb FEC after feeding SL, lambs and adult sheep generally required up to five weeks (Burke et al., 2012a, 2012b; Terrill et al., 2012). This was attributed to initial reluctance of sheep to graze SL mostly as a result of reduced palatability due to astringency (Burke et al., 2012b; Terrill et al., 2012) or sheep requiring a learned response when grazing SL in mixed pastures (Burke et al., 2012b). In that regard, Burke et al. (2012b) observed reduced FEC within two weeks in lambs grazing SL pasture compared to those on bermudagrass. Reduced faecal shedding of eggs reduces pasture contamination with infective larvae thereby indirectly influencing intake and establishment of GIN in the gut of grazing animals (Hoste et al., 2012; Min et al., 2004; Shaik et al., 2006; Terrill et al., 2012). However, the effect of SL on GIN infection in animals is transient and not permanent as animals often exhibit increased FEC when removed from SL (Lange et al., 2006; Min et al., 2004; Shaik et al., 2004; Terrill et al., 2007). It is, therefore, important to consider the feeding duration of SL in the optimisation of feeding strategies to control GIN whilst enhancing growth performance.

As previously alluded to, drying and pelletising SL could reduce its astringency and improve feed intake, feeding these forms of SL could translate into faster turnaround time in reducing FEC of sheep (Table 4). However, using high temperatures during the pelleting process may result in chemical degradation and polymerisation of some bioactive compounds and subsequently, loss of biological activity which could render SL ineffective for controlling GIN (Gujja et al., 2013; Terrill et al., 1990, 1989). Although pelleting SL reduced extractable CT concentrations, the plant's helminth suppressing properties were not affected in small ruminants, whether fed as the primary diet or supplement to grass pastures (Gujja et al., 2013; Kommuru et al., 2015, 2014; Terrill et al., 2007). In addition to temperature control, careful consideration to retain leaves is important when drying and pelletising SL, because the leaves contain higher CT and protein content than other vegetative parts (Mechineni et al., 2014; Donnelly and Anthony, 1973; Petersen et al., 1991; Terrill and Mosjidis, 2017), which not only affect helminth responses, but also growth and immunity. Blood-sucking worms, especially *H. contortus* increase the loss of endogenous proteins from the host's abomasum (Alba-Hurtado and Muñoz-Guzmán, 2013; Cériac et al., 2019; Holmes, 1987). Therefore, moderate to high protein content of SL could be crucial in fighting GIN by replenishing these proteins and subsequently reducing the level of hypoproteinaemia and anaemia through increased haematological regeneration

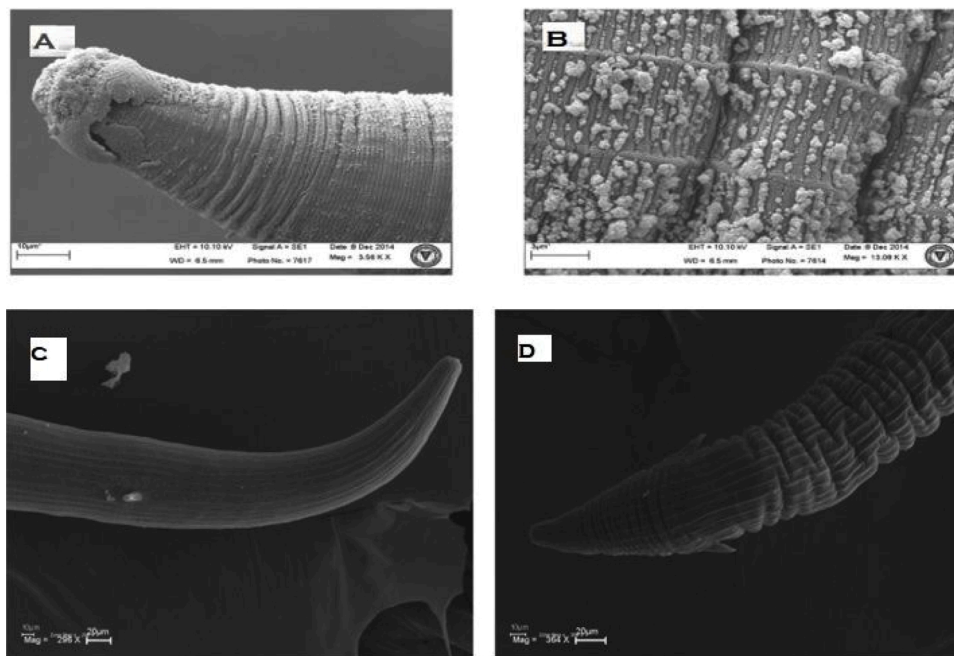


Fig. 2. Scanning electron microscopic images of the buccal area (A), cuticle of the body (B) and anterior end (C and D) of adult *Haemonchus contortus* exposed to condensed tannins. Reprinted from Barone et al. (2018) and Kommuru et al. (2015) with permission from Elsevier.

capacity of bone marrow (Ceï et al., 2018; Cériac et al., 2019).

The mechanism of action through which SL exerts helminth suppressant effects could rely on the indirect effects of CT for their role in enhancing nutrient utilisation when fed in moderate concentrations resulting in improved nutritional status thereby strengthening the host's immune function (Hoste et al., 2012; Moore et al., 2008; Terrill and Mosjidis, 2017). Dietary exposure to SL improved immune response in does (Min et al., 2005) and has been linked with increased blood packed cell volume for small ruminants (Table 4), indicative of greater tolerance to nematode infections (Burke et al., 2011; Gujja et al., 2013; Moore et al., 2008). Alternatively, CT directly reduced blood-sucking by GIN, fecundity of adult female worms, establishment of eggs to infective larvae and survival of adult worms (Castañeda-Ramírez et al., 2019; Kommuru et al., 2015; Martínez-Ortiz-de-Montellano et al., 2013), but this may vary with the CT source, target nematode species, and its development stage (Barone et al., 2018; Hoste et al., 2012).

Utility of polyphenols from other plants for prophylaxis of helminthiasis in small ruminants and their mechanisms of action have been reviewed previously (Hoste et al., 2012, 2006; Kearney et al., 2016; Mazhangara et al., 2020). Plant polyphenols have been reported to inhibit nematode eggs from hatching through true ovicidal activity that stops eggs from developing beyond morula stage and inhibition of larval eclosion (Castañeda-Ramírez et al., 2019). For example, Shaik et al. (2006) showed reduced hatchability of *H. contortus* eggs from faecal samples obtained from goats fed SL. Other mechanisms of action may involve the accumulation of aggregate on the cuticle around the buccal area of adult worms (Fig. 2A and B) due to tannin-protein complexes being formed between condensed tannins and glycoproteins on the epicuticle (Barone et al., 2018; Hoste et al., 2012; Martínez-Ortiz-de-Montellano et al., 2013). This could be the case for SL due to the high prevalence of prodelphinidin-type CT, which have high affinity for proteins including proline- and hydroxyproline-rich structures of eggs, larvae and adult nematodes (Kommuru et al., 2015, 2014). Alternatively, ingested tannins by GIN form complexes with proteins of the internal mucosa causing autolysis, inducing internal rupture and expulsion of viscera (Acedo-Ramírez et al., 2019; Athanasiadou et al., 2001). This could explain structural modifications/damages observed on the cuticle, buccal cavity and vulva of *H. contortus* worms obtained from goats supplemented with SL (Fig. 2D). These structural damages and accumulation of aggregate possibly affect worm motility and nutrition, thus reducing their reproduction potential (Barone et al., 2018; Martínez-Ortiz-de-Montellano et al., 2013). Overall, dietary inclusion of SL causes damage to adult worm anatomy, and reduces fecundity and worm burdens in small ruminants, outlining its direct influence on suppressing GIN activity.

8. Effects of feeding sericea lespedeza on small ruminant meat quality

8.1. Effects on carcass characteristics

Currently, there is limited research relating to carcass characteristics of small ruminants fed SL. Mechineni et al. (2020) reported that grazing goats on pure SL or pasture mixed with SL and bermudagrass improved carcass yields up to 10 % compared to grazing bermudagrass alone. On the other hand, Solaiman et al. (2010) demonstrated that partial or complete substitution of Lucerne with increasing levels (10, 20, 30 % of DM; 7, 15, 22 g CT/kg DM, respectively) of SL in pelleted diets had no influence on hot and cold carcass weights or dressing percentage, but reduced subcutaneous fat thickness. Condensed tannins increase plasma growth hormone levels, which may enhance nitrogen retention and reduce carcass fat deposition and turnover (Solaiman et al., 2010; Turner et al., 2015). The reported subcutaneous fat thickness is within the range proposed as the minimal thickness for goats (Turner et al., 2015). Furthermore, the dressing percentage (Table 5) was comparable to that reported for the same breed of goats supplemented with pine bark (Reynolds et al., 2020), thus, highlighting the potential of SL as alternative feed for meat production.

Even though the influence of SL on sheep carcass characteristics appears to be minimal (Solaiman et al., 2010; Turner et al., 2015), Fair (2014) noted that finishing lambs on SL supplemented diets resulted in improved income over feed costs. This could have been due to improved slaughter and carcass weights. Overall, given potential to enhance growth and carcass characteristics, partial or complete substitution of Lucerne hay with SL hay up to 75 % of total diet, as fed, presents an opportunity to improve the profitability of small ruminants.

Table 5
Influence of dietary supplementation with sericea lespedeza on selected carcass and meat quality attributes of goats.

Attributes ¹	Mean ± SE
Dressing percentage	38.7 ± 0.30
Cooking loss	19.6 ± 1.07
Crude protein	24.7 ± 0.43
Fat	2.71 ± 0.53
Ash	1.83 ± 0.23
Lightness (L*)	46.5 ± 1.77
Redness (a*)	10.2 ± 0.30
Yellowness (b*)	14.1 ± 0.64
Warner-Bratzler shear force (kg)	4.80 ± 0.43

¹ Except for dressing percentage, means were reprinted with permission from Lee et al. (2012). Copyright (2012) American Chemical Society. Dressing percentage is an average of values obtained from Solaiman et al. (2010).

8.2. Effects on physicochemical meat quality

Different physicochemical quality of *longissimus thoracis et lumborum* muscle obtained from goats fed SL have been evaluated (Lee et al., 2012; Turner et al., 2015; Table 5). For instance, the CP and ash contents are comparable to values reported for goat meat, whereas intramuscular fat is lower (Turner et al., 2015). Low intramuscular fat content could partly explain low cooking loss values (Table 5). Cooking loss is, however, also affected by ultimate pH and water-holding capacity (Liu et al., 2016; Ngambu et al., 2013), which were not reported for goats fed SL. Overall, research show that condensed tannin-rich feeds do not influence meat pH (Chikwanha et al., 2019b; Francisco et al., 2018, 2015).

Warner–Bratzler shear force values of meat from goats fed SL hay did not differ from those fed bermudagrass hay (Lee et al., 2012; Mechineni et al., 2020). These values are comparable to those observed for lambs fed Lucerne or other tannin-containing legumes (Francisco et al., 2018, 2015; Girard et al., 2016). On the contrary, current research suggests that dietary supplementation of ruminants with polyphenolic-rich diets may reduce meat tenderness (Tayengwa et al., 2020). Ideally, polyphenolic compounds may interfere with early post-mortem proteolysis of meat by activating high levels of calpastatin, which inhibits activity of μ -calpains, or increasing cross-linking of myofibrillar proteins thereby reducing proteolysis required for meat tenderisation (Francisco et al., 2018; Lund et al., 2011). However, Girard et al. (2016) observed that feeding lambs with condensed tannin-rich legumes did not influence the percentage of non-autolysed μ -calpain and relative μ -calpain activity post-mortem, suggesting that differences in proteolysis rate were not caused by the calpain system. Proteomic analyses demonstrated degradation of desmin and troponin-T proteins complex and phosphorylation isoforms of fast myosin heavy chain (MHC2) patterns which were associated with improved lamb meat tenderness following dietary supplementation with different polyphenolic sources (della Malva et al., 2017). There is consensus that polyphenols may have a strong impact on muscle proteome biomarkers affecting post-mortem proteolysis and tenderisation (Malheiros et al., 2019; Schilling et al., 2017). Therefore, research to determine influence of polyphenols in SL on meat tenderness biomarkers at proteome level is important.

Lee et al. (2012) found dietary supplementation of SL to have no effect on meat colour. This is contrary to reports that inclusion of polyphenols in ruminant diets produce lighter meat colour due to lower haemoglobin and myoglobin content (Priolo et al., 2005). Recent research shows that CT improve meat lightness by reducing microbial biosynthesis of vitamin B₁₂, a precursor for haem pigment synthesis (Liu et al., 2016; Priolo and Vasta, 2007). Feeding diets rich in CT in previous studies (Liu et al., 2016; Priolo et al., 2005) showed normal ranges that consumers associate with acceptable lamb meat colour (Khlijji et al., 2010). Overall, dietary supplementation with SL up to 75 % of the diet as fed enhanced carcass attributes without compromising physicochemical meat quality.

Table 6
Fatty acid composition of chevon obtained from kids fed sericea lespedeza hay.

Fatty acids, FA (% of total FA)	Sericea lespedeza hay #
10:0	0.10
12:0	0.10
14:0	1.68
14:1 n-5	0.13
15:0	0.43
16:0, iso	0.94
16:0	27.2
16:1, trans	0.72
16:1 n-7	1.76
17:0	1.44
17:1	1.28
18:0	5.85
18:1, trans	1.27
18:1 n-9	6.23
18:2 n-6	17.3
18:2	0.18
18:3 n-3	15.9
20:0	0.13
20:1 n-9	0.48
21:0	0.44
22:0	0.12
20:4 n-6	1.18
Total SFA	29.0
Total PUFA	13.2
Total MUFA	16.3
Total n-3	15.91
Total n-6	17.3
PUFA:SFA	0.46
n-6:n-3	1.08

Fatty acids expressed as weight percentage of fatty acid methyl esters.
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8.3. Effects on fatty acids, volatile and sensory profiles of meat

The fatty acid profile of meat obtained from goats fed SL is shown in Table 6. Dietary supplementation with 75 % SL (65 g CT/kg DM) did not influence fatty acid profiles of goat meat (Lee et al., 2012). This could be related to low dosage, type of CT, and possible resistance of ruminal microorganisms to CT (Lee et al., 2012; Patra and Saxena, 2011). Given that SL comprises of up to 98 % high molecular weight prodelphinidin CT, it was anticipated that they would complex with lipids and proteins thereby reducing lipolysis through protecting lipids within protein-phenol complexes, thus making substrate unavailable for lipolytic enzyme degradation (Vasta et al., 2019). Overall, meat from ruminants exposed to moderate dietary polyphenols contain high proportions of health-promoting polyunsaturated fatty acids (PUFAs) and their biohydrogenation intermediates (Francisco et al., 2018; Vahmani et al., 2020; Vasta et al., 2019). This is ascribed to selective inhibition of Group B bacteria (e.g., *Clostridium proteoclasticus*) responsible for converting vaccenic acid to stearic acid, without influencing Group A bacteria (e.g., *Butyrivibrio fibrisolvens*), which converts linoleic acid and α -linolenic acid to vaccenic acid (Min and Solaiman, 2018; Vahmani et al., 2020; Vasta et al., 2019). Polyphenols may interfere with microbial cell walls through substrate deprivation and alteration of membrane permeability systems, thus, retard growth and metabolism of rumen microbes responsible for biohydrogenation (Mueller-Harvey et al., 2019). Polyphenols also complex with unsaturated fatty acids and protect them from biohydrogenation in the rumen making them inaccessible to rumen microbes or their enzymes (Vahmani et al., 2020; Vasta et al., 2019). Overall, the activity of polyphenols increased ruminal outflow of PUFAs and their biohydrogenation intermediates reaching the duodenum for subsequent absorption and deposition in fat depots (Chikwanha et al., 2018; Vahmani et al., 2020; Vasta et al., 2019). To this end, further research to determine optimal feeding strategies and inclusion levels at which SL could promote deposition of health beneficial fatty acids in small ruminant meat is crucial.

Common volatile compound groups isolated from chevon obtained from SL-fed goats were aldehydes, ketones and lactones (Lee et al., 2012). These compounds are formed mostly from oxidation and thermal degradation of unsaturated fatty acids and amino acids (Mottram, 1998). Although only few volatile compounds were isolated, results were comparable to those reported for small ruminant meat fed diets rich in polyphenols (Brognia et al., 2014; Luo et al., 2019; Paleari et al., 2008). Volatile compounds derived from lipid oxidation are associated with off-odours and off-flavours of cooked meat (Mottram, 1998). To the authors' knowledge, there are no studies documenting the impact of dietary supplementation with SL on meat sensory profile, thus warrant investigation. This is particularly important because the plant polyphenolic compounds have been reported to influence the formation of volatile compounds such as indole and skatole (3-methylindole), and enhance the oxidative and microbial stability of meat, consequently preventing the development of meat off-flavours and off-odours (Girard et al., 2016; Jerónimo et al., 2016; Priolo et al., 2009; Priolo and Vasta, 2007).

8.4. Effects on oxidative and microbiological stability of meat

Dietary inclusion of legumes rich in vitamin E and polyphenolic compounds are known to inhibit or delay meat colour deterioration during storage resulting in extended shelf life (Baldi et al., 2019; Bellés et al., 2018; Luciano et al., 2019). Direct mechanism through which polyphenolic compounds influence fresh meat colour stability could rely on enhancement of myoglobin resistance to oxidative deterioration and/or augmentation of overall antioxidant capacity (Aziz and Karboune, 2018; Cunha et al., 2018; Luciano et al., 2019). However, there are no studies investigating the influence of dietary SL on the oxidative stability of meat during shelf storage.

In addition to unhygienic practices during slaughter, carcass or meat contamination are correlated with prevalence of pathogenic bacteria including *E. coli* in the faeces (Elder, 2000; Jacob et al., 2013; Mersha et al., 2010), as influenced by diet (Callaway et al., 2003; Kudva et al., 1997). Although Lee et al. (2009) found that the concentration of *E. coli* was high in the rumen of goats fed SL hay, there were no differences in *E. coli* and total coliform counts in faecal samples when compared with goats fed bermudagrass. Mechineni et al. (2020) reported that faecal *E. coli* counts of goats grazing SL were at least 1.5 log₁₀ coliform units per gram (CFU/g) lower than those of goats grazing mixed pasture consisting of bermudagrass and SL. From these studies it would be expected that similar (Lee et al., 2009) or improved (Mechineni et al., 2020) microbial profiles of meat would be expected following hygienic slaughter procedures (Lee et al., 2009). However, Mechineni et al. (2020) found no dietary influence of SL on carcass *E. coli*, total coliform and aerobic plate counts. It could be essential to investigate the influence of dietary SL on meat microbial stability during shelf-storage. This is important because dietary supplementation with polyphenolic-rich plants have been shown to enhance shelf life by reducing the accumulation of foodborne pathogens including *E. coli*, *S. aureus*, *Campylobacter jejuni*, *Enterobacteriaceae*, *Listeria monocytogenes*, *Pseudomonas* species, and *Salmonella typhimurium* (Aziz and Karboune, 2018; Chikwanha et al., 2019a).

9. Implication for sustainable utilisation of sericea lespedeza on the meat industry

The invasive nature and adaptability of SL to varied edaphoclimatic conditions, high yields, nutrient and phytochemical contents, present an opportunity for its use as a sustainable natural feed ingredient, anti-bloat agent, helminth suppressant and meat preservative for small ruminants. Currently, commercial producers in South Africa trade SL for US\$80/ton compared to US\$130/ton for Lucerne, the most used protein source, which reflects its potential as a low-cost feed source. Moreover, reduced susceptibility to development of resistance by GIN and ruminal methanogens makes it an efficacious alternative to synthetically manufactured anthelmintics and conventional feed sources. To this end, SL could be adopted to potentially reduce costs and/or negative impacts associated with utility of synthetic anti-bloat agent, anthelmintics, feed supplements and meat preservatives while reducing GHG emissions and small ruminant carbon footprint. Although utility of SL may be limited by high fibre and CT contents, its nutritional, helminth suppressant, biopreservative and environmental benefits will be realised when strategies to optimise and mitigate the

challenges associated with these compounds are developed.

From a consumer's perspective, dietary supplementation with SL may influence their purchasing decisions through enhanced meat quality. Delayed onset of microbial growth, myoglobin, lipid and protein oxidation helps to maintain the nutritional and sensory quality of meat for prolonged periods (Apak et al., 2016; Cunha et al., 2018; Luciano et al., 2019). Enhanced shelf stability of meat could leverage producers' ability to distribute meat to distant niche markets (Mlambo and Mapiye, 2015; Tayengwa and Mapiye, 2018). Overall, feeding SL may contribute towards meat healthfulness and safety by improving proportions of health-promoting fatty acids, and reducing incidence of meat-borne pathogens and deleterious additive effects of synthetic anthelmintics and preservative residues, respectively. To this end, it is critical to investigate the influence of feeding SL on keeping and eating qualities of meat.

10. Conclusions

Based on the established evidence provided in the current review, SL could be a sustainable natural feed ingredient and helminth suppressant with potential for producing healthful meat with extended shelf life. This is instrumental in achieving some aspects of food and nutrition security, human health and wellbeing. It is, however, pertinent to determine optimum feeding strategies and inclusion levels at which SL could be used as a functional feed. Overall, to commercially exploit SL as a novel sustainable feed resource for small ruminants, research should focus on simultaneously evaluating its direct impacts on animal health, and yield, physicochemical, keeping and eating qualities of meat.

Author's contribution

CM, AOA and MCM conceptualized the study and acquired funding; LNM drafted the manuscript with editorial inputs from CFLK, OCC, AOA, MCM and CM.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

All authors declare that there are no actual or potential conflicts of interest including financial, personal or other relationships with other people or organizations that could inappropriately influence, or be perceived to influence, this work.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.anifeedsci.2020.114688>.

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