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Review

Nutraceutical Potential of the Low Deciduous Forest to Improve Small Ruminant Nutrition and Health: A Systematic Review

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Simple Summary: There is strong interest in identifying plant species with potential benefits for small ruminant production systems but, despite its importance, there are limited reports systematically exploring such properties. Previously, we proposed an interdisciplinary approach to evaluate the nutraceutical properties of plant species under a heterogeneous context, such as the low deciduous forest. Continuing this effort, we present here a systematic review gathering two decades of research devoted to identifying plant species from such an ecosystem that could influence the nutrition and health of sheep and goats. Encouragingly, the evaluation of plant species from diverse agroecosystems has steadily increased, resulting in the identification of some candidates with nutraceutical properties. Under the heterogeneous conditions of the low deciduous forest, small ruminants consume up to 61 plant species in their grazing circuits. Amongst these, 13 have been tested in in vitro and/or in vivo trials, showing promising properties for both enhancing nutrition and controlling gastrointestinal nematode infections. The objective of this review was to gather relevant information supporting the revalorization and potential use of plants that naturally occur in the tropical forest, which could enhance small ruminants' welfare and production.

Abstract: Nutraceuticals are defined as livestock feeds that combine their nutritional value with their beneficial effects on animal health. We analyzed the outcomes from nearly 20 years of research assessing the nutraceutical properties of plants consumed by sheep and goats in low deciduous forests. A systematic review of different databases suggested 31 peer-reviewed manuscripts according to pre-established criteria. Amongst these, 16 manuscripts described in vitro evaluations investigating the bioactivity of plant secondary compounds in the extracts of 12 plant species. Most of these studies used the abomasal nematode *Haemonchus contortus* as the parasite model. Meanwhile, 11 manuscripts reported in vivo trials under controlled pen conditions, evaluating the relationships between the intake of leaves from different plant species and their secondary compounds and animal nutrition, performance, and gastrointestinal nematode infections. Additionally, four manuscripts described studies under natural feeding conditions. Altogether, the studies showed the inherent complexity of the relationship between small ruminants, plants, nutrients, secondary compounds, and gastrointestinal nematodes in natural feeding systems. Several plant species can be considered good candidates for nutraceutical use. Our findings warrant future work to understand the relationship between plants, ruminants, and their parasites, with the aim to improve the sustainability of production systems based on the native vegetation of tropical forests.

Keywords: anthelmintic plants; bioactive compounds; gastrointestinal nematodes; goat; native vegetation; nutraceutical; plant secondary compounds; sheep; sustainable grazing system

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1. Introduction

The low deciduous forest (LDF) is a heterogeneous vegetation system that predominates in the tropical regions of México [1,2]. This ecosystem covers ~8% of the country's surface area and is a feature in 15 of 32 states of the country [3,4]. The LDF plant inventory is ample, with some studies reporting the existence of up to 2200 plant species [5], of which the Fabaceae (Leguminosae) family is the most abundant [6]. From this large biodiversity, decades of experimentation have allowed researchers to identify approximately 260 plant species as potential feed resources for ruminant livestock [7]. Recent studies have determined the consumption of up to 61 plant species of the LDF by sheep and goats [8,9]. Under this context, the LDF represents a valuable resource for small ruminant production systems in several regions of México where a large majority of small ruminant herds depend exclusively on this vegetation system as their feed source [7,10–12]. Therefore, deeper insight into the relationship between herbivores and the environment can help to design, develop, and improve resilient forage–livestock systems, which could finally enhance ruminant production (Figure 1).

Figure 1. A brief depiction of the natural scenario in the low deciduous forest. Within this heterogenous context, temperature/solar radiation ( ), humidity ( ), and rainfall ( ) are variable throughout the year. Approximately, 260 plant species have been considered as valuable resources for ruminant feeding. There are 80 plants verified as consumed by sheep and goats through direct observation. Each one containing different levels and concentrations of nutrients ( ), plant secondary compounds like terpenes ( ), alkaloids ( ), and phenolic compounds ( ). In addition, there are other components making part of the grazing paddock such as gastrointestinal nematodes' eggs ( ), and infective larvae ( ). Other herbivores such as domestic cattle, white-tailed deer (Odocoileus virginianus yucatanensis), reptiles, birds, and insects are part of the landscape. Also, farmer management and human (non-farmer) impacts are important factors which must be studied and understood in order to improve its utilization and design more sustainable production systems in this "ever-changing" environment.

The term nutraceutical has been coined by combining the word "nutritional" with "pharmaceutical", and it represents "any livestock feed which combines nutritional value with beneficial effects on animal health" [13–15]. This implies that its validation depends on the development of methodologies capable of identifying both the nutritional and pharmaceutical properties of a given resource. However, these two aspects are not the only ones associated with animal performance in complex production systems. Biotic and abiotic factors (either from the ecosystem itself or arising from farmer management) should also be considered, as they could influence the performance of sheep and goats. Plant secondary compounds (PSCs) and gastrointestinal nematodes (GINs) are unavoidable components of the LDF ecosystem, as they mediate its interactions with herbivores [16–18]. The PSCs play a vital role in plant defense and provide plasticity that allows for the interactions of the plants with their environment [19–21]. They are broadly categorized into three functional groups: (i) alkaloids, with up to 20,000 reported molecules [22], (ii) terpenes, with up to 80,000 molecules [23], and (iii) phenolic compounds, with up to 8000 molecules [24]. Within the last group, condensed tannins (CTs) are the most studied PSCs in relation to the nutrition and health of ruminant livestock [25–27]. The bioactive properties of CTs against helminth infections [28–30] and the capacity of CTs and GINs to modulate methane production at a ruminal level [31–33] have been recently explored.

In the present review, we focused on the anthelmintic effects of PSCs because GIN infections are also a common feature in grazing ruminant production systems [34,35]. GIN infections are currently considered one of the main drawbacks for small ruminant productive systems worldwide [36–38]. Considering the above, proper and systematic validation of the nutraceutical properties of plant species should merge the nutritional and sanitary effects by studying the relationships between ruminants, their GINs, and the macronutrient/PSC content of plants.

Recently, we presented an interdisciplinary proposal to identify plant species with nutraceutical potential using small ruminants and their GIN infections as a model [39]. Broadly, the methodology established that the nutraceutical validation of plant materials should involve disciplines such as botany, ecology, agronomy, ethology, ethnoveterinary, nutrition, parasitology, and chemistry. The general process, which is outlined in Figure 2, is briefly structured in ten steps, described as follows: (i) identify and classify the plant species occurring in the field, (ii) assess the plants' biomass availability, (iii) confirm—by ethnoveterinary or direct observation—those plants freely consumed by animals, (iv) estimate the selection of plant species, (v) perform a chemical characterization of the plant material, including nutrients and PSCs, (vi) evaluate the plants' digestibility with in vitro or in vivo techniques, (vii) establish techniques for PSC purification using specific solvents, (viii) evaluate the bioactive effect of extracts using in vitro parasitological tests in different stages of the biological cycle of GINs, (ix) perform in vivo trials under controlled—single choice or cafeteria—conditions, and (x) carry out field in vivo trials that take into consideration the natural behavior of small ruminant species.

In the present work, we present a systematic review on the efforts to evaluate both in vitro and in vivo nutraceutical feed resources from such a heterogeneous vegetation scenario, with the aim to encourage future research that deepens our knowledge of the relationships between small ruminants, their GINs, plants' nutrients, and PSCs, thus contributing to the revalorization of native vegetation systems.

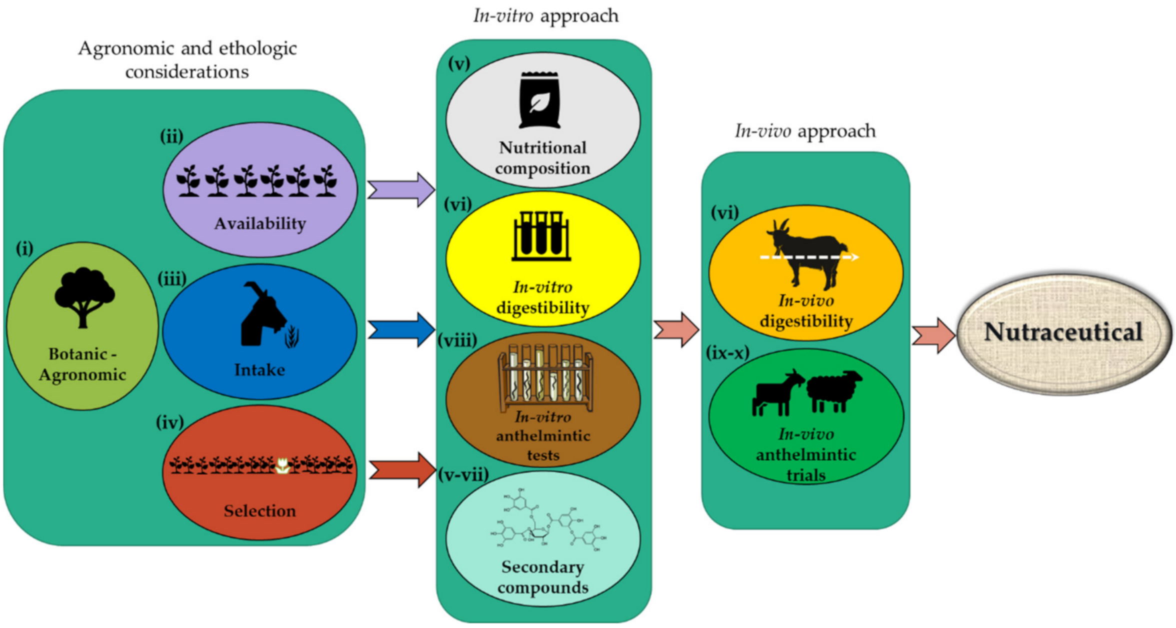

Figure 2. The ten-step proposed protocol for the identification of plants with nutraceutical potential. The parentheses represent each step mentioned above. A cyclic conceptualization, where each component provides feedback to the other, was presented by Torres-Fajardo et al. [39].

2. Methods

The process of the search and classification of bibliographic material began on 1 March 2020, a last search was performed on 1 February 2021. The web-based search comprised databases such as the Wiley Online Library (https://onlinelibrary.wiley.com/, accessed on 15 May 2021), Springer Link (https://link.springer.com/, accessed on 15 May 2021), Science Direct (https://www.sciencedirect.com/, accessed on 15 May 2021), PubMed (https://pubmed.ncbi.nlm.nih.gov/, accessed on 15 May 2021) and the Multidisciplinary Digital Publishing Institute (https://www.mdpi.com/, accessed on 15 May 2021). The database Scielo (https://scielo.org/es/, accessed on 15 May 2021) was considered for searching manuscripts in Spanish and Portuguese languages.

For the data collection, the following keywords were used: "low deciduous forest OR tropical deciduous forest", "anthelmintic activity OR anthelmintic plants OR bioactive plants", "plant secondary compounds OR plant secondary metabolites", "nutraceuticals", "gastrointestinal nematodes", "sheep", and "goats". The authors selected and reviewed the manuscripts to meet the pre-established inclusion criteria, as follows: (i) studies involving small ruminants (sheep and/or goats), (ii) studies evaluating plant species from an LDF, (iii) studies involving GIN species of small ruminants, (iv) in vitro studies specifying solvents/methods for PSC extraction, (v) in vitro studies reporting the use of parasitological techniques to evaluate the bioactivity of compounds on specific stages of the GIN biological cycle, (vi) in vivo studies considering a patent GIN infection, and (vii) in vivo studies administering foliage or extracts from LDF plant species. This search methodology resulted in 31 original peer-reviewed manuscripts fulfilling the criteria.

3. Results

The literature search produced 31 publications from nearly 20 years of research in the LDF ecosystem. Broadly, the analyzed studies were performed in a tropical subhumid area (Aw_0), with an annual average temperature of 26–27.6 °C, relative humidity of 72%, and an average rainfall of 728–1000 mm. A common feature in the ecosystem is its marked dry season between November and May, causing the shrubs and tree species to lose approximately 70% of their foliage cover. In summary, 16 studies used the in vitro approach on the leaves of plants and are presented in Table 1. In addition, Table 2 includes 11 in vivo studies, with 7 of them evaluating the leaves of a single plant and the remaining 4 using a cafeteria protocol, using the leaves of different plant species. Table 3 shows four in vivo studies performed under the natural field grazing/browsing conditions of the LDF. Finally, Table 4 presents the anthelmintic effect (in vitro and in vivo) of low deciduous forest plant species against different phases of gastrointestinal nematodes' biological cycle.

For the in vitro approach (16 studies), a total of 12 plants were evaluated. The most commonly incorporated species were *Lysiloma latisiliquum* (representing 56% of the studies), *Acacia pennatula* (50%), *Leucaena leucocephala* (37%), *Senegalia gaumeri* (31%), *Havardia albicans* (25%), and *Piscidia piscipula* (25%); all of these plants belong to the Fabaceae family. The Malphigiaceae and Polygonaceae families were also included in two (12.5%) of the studies, while Moraceae and Phytolaccaceae were used in one study. Most studies (81%) used acetone–water (70:30) extracts, while three studies (18%) used methanol–water (70:30) extracts. Other methodologies—or solvents—for extraction aimed at isolating certain PSCs of interest, such as flavonoids, terpenoids, triterpenoids, coumarins, saponins, flavonoid glycosides, and alkaloids. Usually, the CTs were the target PSCs that were mostly studied (81%). The screening of alkaloids, flavonoids, and saponins was considered in 12% of the studies. Regarding the GIN species used for the in vitro screening, 93% (15/16) of the studies used the abomasal nematode *Haemonchus contortus*, while the intestinal nematode *Trichostrongylus colubriformis* was used in one study. The larval exsheathment inhibition test (LEIT) was the most employed test (56%), followed by the larval motility inhibition test (LMIT) (44%), and the egg inhibition test (EHT) (37%).

In the in vivo approach, which included 11 controlled experiments, goats were used in 63% of occasions (7/11), while sheep were used in 36% of the experiments (4/11). The mean body weight (± standard deviation) of experimental animals was 16.8 ± 8.36 kg. Monospecific infection with the abomasal nematode *H. contortus* was employed in nine studies (81%), while a natural *H. contortus* infection and a mixed infection of *H. contortus* plus *T. colubriformis* were studied in one trial each. Similar to the in vitro approach, the main target PSCs of the in vivo studies were the CTs, representing 81% of the trials. Within the ten plants used under this approach, *L. latisiliquum* was the most frequently used (45%), followed by *G. floribundum* (36%), *H. albicans* (36%), and *L. leucocephala* (27%). The shrub *A. pennatula*, which was the second-most used resource in in vitro trials (used in seven studies), was only tested once in an in vivo trial. The four studies that were performed under natural feeding conditions took place during the rainy season, when plant species have more biomass. All these studies used a natural GIN infection—mainly composed of *H. contortus*, *T. colubriformis*, and *Oesophagostomum columbianum*. In addition, all studies implemented a direct observational methodology with the aim of quantifying the voluntary feed intake of experimental animals [40,41].

Table 1. Screening the in vitro anthelmintic activity against small ruminant's gastrointestinal nematodes using different extracts produced from the leaves of plant species present in the low deciduous forest.

Plant(s)	Family	Type of Solvent	PSC Type	GIN Species (Isolate(s) Origin)	Type of Assay	Salient Results	Reference
Acacia pennatula *Leucaena leucocephala* *Lysiloma latisiliquum* *Piscidia piscipula*	Fabaceae	Acetone–Water (70:30)	CT PVPP	*Haemonchus contortus* (French isolate)	LMIT LEIT	The four extracts showed good results in LEIT. In LMIT, *P. piscipula* did not show activity.	[42]
Havardia albicans *Senegalia gaumeri*	Fabaceae	Acetone–Water (70:30)	CT	*H. contortus* (Mexican temperate isolate)	LMIT	*S. gaumeri* did not have an effect against larvae motility.	[43]
A. pennatula *L. leucocephala* *L. latisiliquum* *P. piscipula*	Fabaceae	Acetone–Water (70:30)	CT PVPP	*Trichostrongylus colubriformis* (French isolate)	LMIT LEIT	The four extracts showed good results in LEIT. In LMIT, *P. piscipula* did not show activity.	[44]
A. pennatula *L. leucocephala* *L. latisiliquum* *P. piscipula*	Fabaceae	Acetone–Water (70:30)	CT PVPP	*H. contortus* (Temperate and tropical Mexican isolates)	LMIT	Sensitivity of *H. contortus* strains was related with their origin as well as the contact with tannin-rich plants.	[45]
H. albicans *L. leucocephala* *S. gaumeri*	Fabaceae	Acetone–Water (70:30)	CT	*H. contortus* (French isolate)	LMIT LEIT	*S. gaumeri* and *H. albicans* were more potent inhibitors of larvae biology.	[46]
Brosimum alicastrum	Moraceae						
Phytolacca icosandra	Phytolaccaceae	E, DCM, n-H	F, St, T, A, C, Sp ¤	*H. contortus* (Temperate Mexican isolate)	EHT LMIT	Extracts' bioactivity on both assays was E > DCM > n-H.	[47]
L. latisiliquum	Fabaceae	Acetone–Water (70:30)	CT	*H. contortus* (Mexican and French isolates)	ANM	CTs formed aggregates in the buccal capsule, female vulva, and anus.	[48]
L. latisiliquum	Fabaceae	Acetone–Water (70:30)	CT PVPP	*H. contortus* (Temperate Mexican isolate)	EHT	Blocking CTs with PVPP increased the AH effect of the extract. First work using EC_{50} values.	[49]
A. pennatula	Fabaceae	Acetone–Water (70:30)	CT PVPP	10 isolates of *H. contortus* §	EHT	A tropical Mexican—but not local—strain was the least susceptible against extract.	[50]
A. pennatula	Fabaceae	Acetone–Water (70:30)	CT	*H. contortus* L_3 from 1 to 7 weeks of age (Tropical Mexican isolate)	LMIT LEIT LMOT	EC_{50} and EC_{90} of L_3 were different: w1 < w2 = w3 = w4 = w5 < w6 = w7.	[51]

Table 1. *Cont.*

Plant(s)	Family	Type of Solvent	PSC Type	GIN Species (Isolate(s) Origin)	Type of Assay	Salient Results	Reference
Acacia collinsi *A. pennatula* *H. albicans* *L. leucocephala* *L. latisiliquum* *Mimosa bahamensis* *P. piscipula* *S. gaumeri*	Fabaceae	M–W 70:30	CT, PP PVPP	*H. contortus* (Tropical Mexican isolate)	EHT LEIT	Positive correlations were found between the EC50 of extracts and their CT and TP contents in the EHT.	[52]
Bunchosia swartziana *Gymnopodium floribundum*	Malpighiaceae Polygonaceae						
A. pennatula	Fabaceae	Acetone–Water (70:30)	CT PVPP	10 isolates of *H. contortus* §	LEIT	Lowest and highest EC_{50} were from a Mexican and a French isolate, respectively (36.44 vs. 501.40 µg/mL).	[53]
L. latisiliquum	Fabaceae	Acetone–Water, M–W, M, E, MChl, DCMSE, EASE, and MSE	FG, quercitrin, arbutin	*H. contortus* (Tropical Mexican isolate)	LEIT	The AH activity against L_3 was A–W > M–W = M = MSE.	[54]
A. collinsi *A. pennatula* *H. albicans* *L. leucocephala* *L. latisiliquum* *M. bahamensis* *P. piscipula* *S. gaumeri*	Fabaceae	Acetone–Water (70:30)	CT	*H. contortus* (Tropical Mexican isolate)	EHT LEIT	Despite their low CT quantities, *S. gaumeri* showed the highest AH effect against GIN eggs and larvae.	[55]
B. swartziana *G. floribundum*	Malpighiaceae Polygonaceae						
L. latisiliquum	Fabaceae	Acetone–Water, and then compared FR, OD, and LP	CT	*H. contortus*	LEIT	The AH activity against L_3 was OD > LP = FR.	[56]

Table 1. *Cont.*

Plant(s)	Family	Type of Solvent	PSC Type	GIN Species (Isolate(s) Origin)	Type of Assay	Salient Results	Reference
S. gaumeri	Fabaceae	M–W 70:30	F, Sp, 3T, A	*H. contortus* (Tropical Mexican isolate)	EHT	Although p-coumaric acid was suggested as a bioactive, it failed to show effects alone.	[57]

Type of solvent: E (ethanolic), DCM (dichloromethane), n-H (n-Hexane), M–W (methanolic–water), M (methanolic), Mch (methanol–chloroform), DCMSE (dichloromethane successive extractions), EASE (ethyl acetate successive extractions), MSE (methanol successive extractions), FR (fresh leaves), OD (oven-dried), LP (lyophilized). Target PSCs: CT (condensed tannins), F (flavonoids), St (steroids), T (terpenoids), C (coumarins), Sp (saponins), PP (polyphenols), FG (flavonoid glycosides), 3T (triterpenes), A (alkaloids), ¤ (assessments were qualitative), ^{PVPP} This super index represents the studies that used polyvinyl pyrrolidone to neutralize CTs and differentiate their effects. GIN (gastrointestinal nematode) species: L_3 (third larvae stage), § (larvae origin: two Mexican from template climates, two Mexican from tropical climates, two from Australia, two from France, one from South Africa, and one from the United States of America). Type of assay: LMIT (larvae motility inhibition test), LEIT (larvae exsheathment inhibition test), EHT (egg hatch test), ANM (adult nematode measurements), LMOT (larvae motility observation test). Salient results: EC_{50} (effective concentration 50), EC_{90} (effective concentration 90), µg/mL (micrograms per milliliter), AH (anthelmintic). w1 (week 1), w2 (week 2), and so forth.

Table 2. Nutritional and parasitological effects reported for sheep or goats when consuming the leaves of different plants from the low deciduous forest in pen studies or cafeteria studies, either with natural or controlled GIN infections.

Scenario	Species	n	Age	Type of Infection. (Isolate(s) Origin)	Plant(s)	PSC Type	Nutritional Effect	Parasitological Effect	Reference
Controlled	Goat	18	6 m	Mixed *Hc, Tc* (Mexican and French isolates)	*L. latisiliquum*	CT ^{PEG}	NR	Total counts of adult GINs were reduced by 70% after *L. latisiliquum* consumption.	[58]
Controlled	Sheep	22	2 m	Monospecific *Hc.* (Temperate Mexican isolate)	*L. latisiliquum*	CT	Higher consumption of *L. latisiliquum* in infected animals.	Lower GIN female size, fecundity, and EPG excretion in infected animals †.	[59]
Controlled	Sheep	21	3 m	Monospecific *Hc.* (Temperate Mexican isolate)	*H. albicans*	CT ^{PEG}	Lower DMD for animals consuming *H. albicans.*	*H. albicans* inclusion reduced the length of female GIN †.	[60]
Controlled	Goat	12	3 m	Monospecific *Hc.* (Temperate Mexican isolate)	*P. icosandra*	C, F, Sp St, T	NR	Significant reduction (72%) of EPG excretion in the treated group.	[61]
Controlled	Sheep	28	3 m	Monospecific *Hc*	*H. albicans*	CT ^{PEG}	Lower DMD for animals consuming *H. albicans.*	Significant reduction (58.8%) of EPG excretion in the treated group.	[62]
Controlled	Goat	4	NR	Monospecific *Hc.* (Mexican and French isolates)	*L. latisiliquum*	CT	NR	Changes in the cuticle, buccal capsule, and cephalic region (assessed by SEM†).	[48]

Table 2. *Cont.*

Scenario	Species	n	Age	Type of Infection. (Isolate(s) Origin)	Plant(s)	PSC Type	Nutritional Effect	Parasitological Effect	Reference
Cafeteria	Goat	12	3–5 y	Natural	*L. leucocephala* *G. floribundum* *M. bahamensis* *Viguiera dentata*	CT	Neither intake nor selection were modified between experimental groups (infected vs. non-infected).	Reduction of 91.1% of EPG excretion in infected goats during the trial.	[63]
Cafeteria	Goat	12	3–5 y	Monospecific *Hc.* (Tropical Mexican isolate)	*A. pennatula* *B. alicastrum* *G. floribundum* *H. albicans* *L. latisiliquum* *L. leucocephala* *M. bahamensis* *P. piscipula*	CT	Neither intake nor selection were modified between experimental groups (infected vs. non-infected).	Reductions of 28.08% and 13.61% of EPG during two experimental periods (5 days each period).	[64]
Cafeteria	Goat	22	NR	Monospecific *Hc.* (Tropical Mexican isolate)	*H. albicans* *G. floribundum* *L. leucocephala* *P. piscipula*	CT ^{PEG}	GIN infection increased CT consumption. PEG administration reduced *L. leucocephala* and CP consumption.	Reduction of 70% of EPG excretion for infected and non-infected goats during the trial.	[65]
Controlled	Goat	4	NR	Monospecific *Hc.* (Tropical Mexican isolate)	*L. latisiliquum*	PP	NR	PP diet caused ultrastructural changes in muscular and intestinal cells, assessed by SEM †.	[66]
Controlled	Sheep	30	3–4 m	Monospecific *Hc.* (Tropical Mexican isolate)	*G. floribundum*	CT	*G. floribundum* inclusion reduced DMD and OMD.	Inclusion of plant at 40% reduced TFEC and number of adult female GINs.	[67]

Age: m (months), y (years), NR (not reported). N: Number of experimental animals. Type of infection: Hc (*Haemonchus contortus*), Tc (*Trichostrongylus colubriformis*). Target PSCs: CTs (condensed tannins), C (coumarins), F (flavonoids), Sp (saponins), St (steroids), T (terpenoids), PP (polyphenol), ^{PEG} This super index represents the studies that used polyethylene glycol to neutralize CTs and differentiate their effects. Nutritional effect: NR (not reported), DMD (dry matter digestibility), GIN (gastrointestinal nematodes), PEG (polyethylene glycol), OMD (organic matter digestibility), CP (crude protein). Parasitological effect: EPG (eggs per gram), SEM (scanning electron microscopy), TFEC (total fecal egg count), † (studies that assessed the relationships between PSC consumption and post-mortem adult nematode measurements).

Table 3. Interactions between the natural gastrointestinal nematode infection and the feeding behavior of sheep or goats when browsing the foliage of the plant species present in the low deciduous forest of México. All the studies were performed during the rainy season (between June and October) and employed a continuous bite monitoring methodology for feeding behavior assessment.

Species	Age	n	GIN Infection Composition	Max EPG Mean	Duration (Months)	Number of Plants Consumed	% CT in Diet	Salient Results	Reference
Goat	5–9 y	12	15.3% Hc 46.1% Tc 38.4% Oc	450	3	35	1.5	Anthelmintic treatment did not modify the macronutrient or CT intake.	[68]
Sheep and goat	4–5 m	24	Hc, Tc, Oc †	NR	3	37	NR	Kids consumed less low-stratum plants and more medium-stratum plants, resulting in lower GIN infections.	[69]
Goat	Adult	36	44% Hc 30% Tc 26% Oc	2450	3.5	45	5–9 PEG	Reduction of 78% of EPG during the first experimental stage. Higher selectivity towards grass species.	[70]
Goat	Adult	12	44% Hc 30% Tc 26% Oc	1300	1	NR	NR	Reduction of 81.2% of EPG during experiment. All goats consumed more grass species in the early mornings.	[71]

Age: m (months), y (years). N: Number of experimental animals. GIN infection composition (composition of natural gastrointestinal nematodes infection); Hc (Haemonchus contortus), Tc (Trichostrongylus colubriformis), Oc (Oesophagostomum columbianum); † (Adult identification was done during necropsy, fecal cultures were not performed). Max EPG mean (maximum mean of gastrointestinal nematode eggs per gram of feces; NR (not reported). Number of plants consumed: NR (not reported). % CT in diet: Percentage of condensed tannins in diet, PEG This super index represents those studies that used polyethylene glycol to neutralize CTs and differentiate their effects, NR (not reported). Salient results: GIN (gastrointestinal nematodes), EPG (eggs per gram), DM (dry matter).

Table 4. Summary of the anthelmintic effect of the low deciduous forest plants species against different phases of gastrointestinal nematodes' biological cycles [1].

Plant Species	Family	In Vitro Tests [2]			Reduction of EPG Counts in In Vivo Trials [3]
		Eggs	Larvae	Adult GIN	
Acacia collinsi	Fabaceae	√	√	nsy	nsy
Acacia pennatula	Fabaceae	√	√	nsy	⍓
Brosimum alicastrum	Moraceae	nsy	√	nsy	⍓
Bunchosia swartsiana	Malpighiaceae	√	√	nsy	nsy
Gymnopodium floribundum	Polygonaceae	√	√	nsy	√
Havardia albicans	Fabaceae	√	√	√	√
Leucaena leucocephala	Fabaceae	√	√	nsy	⍓
Lysiloma latisiliquum	Fabaceae	√	√	√	√
Mimosa bahamanesis	Fabaceae	√	√	nsy	⍓
Phytolacca icosandra	Phytolaccaceae	√	√	nsy	√
Piscidia piscipula	Fabaceae	√	√	nsy	⍓
Senegalia gaumeri	Fabaceae	√	√	nsy	nsy
Viguiera dentata	Asteraceae	nsy	nsy	nsy	⍓

[1] For a more detailed description of this process, as well as other factors involved, please refer to previous tables and consult the references herein. [2] In vitro tests: GIN (gastrointestinal nematodes). √(at least one study has reported some anthelmintic effect over this biological cycle phase), nsy (not studied yet). [3] Reduction of EPG counts in in vivo trials: ⍓ a reduction in eggs per gram (EPG) excretion has been reported, but the study was designed as a cafeteria trial, in which the anthelmintic effect of a given plant should be interpreted cautiously.

4. Discussion

The present work reviews the state of the efforts to evaluate the in vitro and in vivo nutraceutical potential of feed resources from the heterogeneous vegetation of the LDF. After the literature search, we classified and analyzed 31 manuscripts produced in almost two decades of research. It is important to highlight that the screening process of nutraceutical plants in the LDF was partly derived by the search for non-chemical alternatives for the control of GINs in small ruminants, which could help with combating GIN populations resistant to conventional chemical therapy. Anthelmintic products emerged in the 1960s and had a continuous release of novel molecules for three decades [72,73]. During this period, the continuous release of products in the market offered good therapeutic results. However, this strategy is now considered unsustainable on its own [36,74,75]. Anthelmintic resistance leads to poor control of GIN infection, and hence, these parasites still exert profound effects on the nutrition, health, and welfare of their hosts, and consequently threaten the profitability of grazing production systems worldwide [76–78]. Consequently, alternatives to conventional anthelmintic treatment, such as the feeding of PSC-rich plants or the use of their bioactive compounds, have been a matter of intensive research [79–81].

The nutraceutical approach represents an integral view of the plant–animal interactions because it takes into account elements other than PSCs. Although the information gathered when assessing the nutraceutical potential of plants is relevant to develop new production systems or strategies, a thorough methodology for its evaluation in ruminant livestock is still under construction. Benell et al. [82] presented a systematic approach aimed at selecting native Australian plants with bioactive benefits. Later, Hoste et al. [13] established some guidelines for the evaluation of nutraceutical plant materials using different CT-rich legume plants as models, and Torres-Fajardo et al. [39] proposed an interdisciplinary approach used to identify plant species with nutraceutical potential from heterogeneous vegetation scenarios, also using GIN infection as a model. The implementation of the nutraceutical concept on specific plant species has also been considered by Peña-Espinoza et al. [83] in reviewing the potential use of chicory (*Cichorium intybus*) as a nutraceutical forage in parasitized livestock, by Marie-Magdeleine et al. [84] in evaluating the nutraceutical potential of pelleted *Leucaena Leucocephala* leaves in goat kids, and by Oliveira et al. [85] in reviewing the use of Mediterranean salt-tolerant plants as nutraceuticals or phytotherapeutics in ruminants. In the following discussion, we tackle the studies that have collectively evaluated the nutraceutical value of LDF plant species.

4.1. The In Vitro Experiences

The use of in vitro studies as part of a nutraceutical screening process of LDF plants was first reported in 2008 by Alonso-Díaz et al. who studied the effect of four tannin-rich plant extracts against two fundamental processes of the infective larvae (L_3): motility and exsheathment. In this first study, the L_3 of the abomasal *H. contortus* [42] and the intestinal *T. colubriformis* [44] GIN species (French isolates) were used and showed that *A. pennatula, L. latisiliquum*, and *L. leucocephala* at 1200 micrograms per milliliter (µg/mL) had anthelmintic activity, as measured with the larval migration inhibition test (LMIT), while *P. piscipula* did not show such properties. On the contrary, all the plant extracts showed anthelmintic activity in the larval exsheathment inhibition test (LEIT). Subsequently, *S. gaumeri* and *H. albicans* extracts were tested using the LMIT [43,46] and LEIT [46], showing that *H. albicans* caused a reduction of 48 and 68.9% in the L_3 motility at 1200 and 2400 µg/mL, respectively. Meanwhile, *S. gaumeri* showed no effect as per the LEIT [43], but a reduction of 20.9% in the LMIT [46]. Given that all extracts exerted activity against exsheathment at 300 µg/mL in the latter study, it was concluded that the LEIT was more sensitive compared with the LMIT.

The egg hatching test (EHT) was initially performed by Hernández-Villegas et al. [47], but the work of Vargas-Magaña et al. [49] suggested that the main effect of *L. latisiliquum* acetone–water (A–W) extracts was to prevent the larvae eclosion from eggs, which is the final step in the hatching process. This mechanism was later confirmed with *A. pennatula* extracts [50]. The proposed mechanism to explain this activity includes the inhibition of enzymes, the binding of egg-structural proteins, the binding of receptors, or a synergy between these processes [86,87]. It is worth mentioning that Calderón-Quintal et al. [45] and Chan-Pérez et al. [50,53] provided the first evidence of variation in susceptibility according to the GIN geographic origin. In the first work, differences in susceptibility were evidenced in three *H. contortus* strains from different regions of México. Strains from tropical México, which, in principle, have been in frequent contact with tropical CT-rich plants due to their regular intake by sheep and goats while browsing the LDF, were less sensitive to the extracts compared to the strain from a temperate zone of México. In the second and third works, the same tendency was found when using *A. pennatula* extracts against ten *H. contortus* isolates from diverse geographical origins (two from temperate climates in México, two from tropical climates in México, two from Australia, two from France, one from South Africa, and one from the United States of America). Another striking result that emerged from subsequent studies was the consideration of the larval age as a factor affecting the outcome of in vitro tests in tropical environments [51]. In this case, the LEIT evidenced that one-week-old *H. contortus* infective larvae showed higher motility and susceptibility to extracts, two to five-week-old infective larvae showed a good exsheathment ability, and older infective larvae showed greater exsheathment variability. Considering these results, it was reasonable to recommend the use of two-to-five week-old infective larvae for future studies. A recent study proposed the use of *T. colubriformis* infective larvae no older than 7 weeks of age [88]. As a result, the use of infective larvae, under tropical conditions should within a range of age that challenges the recommendation of three months made by other authors with larvae under temperate conditions [89]. However, a direct implication of this recommendation is the huge challenge that it represents for tropical laboratories, as they would need to produce their biological material constantly [90].

Regarding solvents for the extraction of PSCs, contrasting outcomes were noted by evaluating the bioactivity of ten plant species using methanol–water (M–W; 70:30) [52]. To begin with, the *A. pennatula* extract needed the highest concentrations to inhibit the 50% of egg hatching (EC_{50}: 8180.8 µg/mL) and the 50% of larval exsheathment (EC_{50}: 426 µg/mL). Secondly, *L. leucocephala* and *S. gaumeri* extracts showed the lowest EC_{50} values in the EHT and LEIT (139.9 and 186.3 µg/mL, respectively), albeit they had the lowest CT content among the studied plants. Finally, *H. albicans*, *G. floribundum*, and *S. gaumeri* showed EC_{50} values of 63.5, 66.9, and 184.7 μg/mL, respectively in the LEIT. Castañeda-Ramírez et al. [55] provided the first in vitro proposal to evaluate the nutraceutical value of the ten feed resources used in the previous experiment. In this protocol, the authors evaluated the macronutrient content, the in vitro dry matter, and the organic matter digestibility. The extracts were obtained with acetone–water (A–W; 70:30) solvents and subsequently employed in the EHT and LEIT. The extracts of *S. gaumeri* showed the lowest EC_{50} values in the EHT (401.8 μg/mL) and LEIT (83.1 μg/mL), together with a good macronutrient profile (21.4% crude protein and 17.0% acid detergent fiber), in vitro organic matter digestibility (53.5%), and low CT contents (1.0%). Hence, this plant was used in a forthcoming study with the aim of isolating the metabolites involved in its AH activity through a bio-guided fractionation technique [57]. This methodology allowed the identification of p-coumaric acid—a phenolic compound—as the bioactive molecule. However, when this compound was tested alone, there was no AH effect, suggesting a synergy with other PSCs. Finally, a study performed by Hernández-Bolio et al. [54] used a metabolomic approach on the shrub/tree *L. latisiliquum* and suggested AH effects of highly polar PSCs, such as quercitrin and arbutin. In addition, they compared different polyphenol removal and drying methods, pointing out that CT and their monomers were not related to the in vitro AH activity of *L. latisiliquum* [56]. In this respect, Sandoval-Castro [91] argued that such a lack of effect should be demonstrated by isolating and testing the specific CT fraction of *L. latisiliquum* extract, conferring anthelmintic activity.

4.2. The In Vivo Experiences

The hypothesis linking PSC intake with the potential anthelmintic properties of plants that contain them has been explored since the early 2000s. In the first in vivo publication, Brunet et al. [58] used an artificial infection with GINs and evidenced that the abomasum and first portion of the small intestine of goats fed with *L. latisiliquum* foliage had lower counts of immature *H. contortus* and *T. colubriformis* than those fed with foliage of *B. alicastrum*, a plant with low PSC content (75 ± 23.45 vs. 258.33 ± 74.68, respectively). The authors concluded that the reduction in the establishment was driven by CTs, which avoided the exsheathment of L_3. Meanwhile, Martínez-Ortiz-de-Montellano et al. [59] supplemented artificially infected sheep with *L. latisiliquum* foliage and noted a reduction in the fecal excretion of GIN eggs (eggs per gram, EPG), as well as a reduction in the length and fecundity of adult worms. These above-mentioned studies found no evidence to support the indirect effect of CTs, which have been hypothesized to stimulate an immunological response mediated by an increase in the number of inflammatory cells in the mucosa [92]. Later, the previous positive in vitro effects of *Phytolacca icosandra* [47] led to performing an in vivo trial [61], in which its ethanolic extracts were administered for two consecutive days using gelatin capsules and caused a reduction of 66% of the EPG. Such an effect could not be attributed to any specific PSC, as the extract contained a mixture of coumarins, flavonoids, steroids, terpenoids, and saponins. The foliage of *H. albicans* was also studied by the authors of [60,62]. Both experiments assessed the relationships between voluntary feed intake, dry matter digestibility, and fecal GIN excretion in infected vs. dewormed lambs eating this plant. The inclusion of *H. albicans* caused a reduction of dry matter digestibility in both cases. In the former experiment, fecundity and the size of adult GIN were reduced in animals consuming *H. albicans* [60], and in the latter experiment, lambs consuming this plant increased their voluntary feed intake and showed a reduction of 58.8% of the EPG [62]. A step further in the elucidation of the mechanisms of action of PSCs—specifically CTs—was done by Martínez-Ortiz-de-Montellano et al. [48,66] through the scanning electron microscopy technique. In both works, *L. latisiliquum* foliage was administered to goats artificially infected with *H. contortus* and changes in the structure and ultrastructure of adult worms were measured. These studies allowed for identifying superficial alterations in the cuticle, buccal capsule, and aggregates in the cephalic region, as well as ultrastructural changes, such as vacuolization of the intestinal, muscular, and hypodermal cells.

Cafeteria trials, as part of a nutraceutical screening process, were implemented in two experiments by Ventura-Cordero et al. [63,64]. Both studies evaluated the intake and selection of LDF plants in response to natural [63] or artificial [64] GIN infections using goats with many years of browsing experience. A higher GIN excretion of 2150 EPG did not change either the intake or selection of four plant species in the former study. Thus, in the latter study, the authors decided to superimpose an artificial infection with *H. contortus*. Nevertheless, the same intake pattern was maintained independently of high GIN egg excretions (3158 EPG). In addition, body weight gain, the mean packed cell volume, and the mean hemoglobin levels were not different between the infected and non-infected animals. Due to these findings, Torres-Fajardo et al. [65] evaluated the goats feeding behavior and their relationships with GIN infection, CT intake, and their interactions. It is worth noting that there was an increase in CT intake for GIN-infected goats and a reduction of the crude protein intake in animals that were CT-neutralized by the administration of polyethylene glycol. It is possible that the high GIN excretion in this study (nearly 5000 EPG) triggered the higher CT intake. In addition, the reduction of CP intake in polyethylene glycol-administered goats could be aimed at avoiding an excess of ruminal protein metabolism and their physiological costs. Together, these cafeteria trials allowed researchers to point out that CTs were not the only PSCs with anthelmintic properties and that the ingestive behavior of small ruminants is a multifactorial process.

The study done by Méndez-Ortiz et al. [67] represents the first attempt to validate the nutraceutical value of plants under controlled in vivo conditions. Researchers used the leaves of the shrub/tree *G. floribundum* and assessed its macronutrient and PSC content together with the in vivo dry matter digestibility and organic matter digestibility. The authors administered different plant inclusion levels to hair sheep lambs carrying an artificial *H. contortus* infection. The inclusion of *G. floribundum* at 40% reduced the digestibility but maintain live weight gain and voluntary feed intake. In addition, it significantly reduced the EPG and female GIN burdens in post-mortem measurements. Furthermore, the bioactivity of its extracts against *H. contortus* was confirmed using the LEIT. The authors highlighted the nutraceutical potential of this plant species.

The next scenario implies the evaluation of plants under the LDF feeding conditions. At first, Jaimez-Rodríguez et al. [69] compared the feeding behavior of inexperienced tracer kids and lambs and observed the consumption of 37 plants species. In addition, kids had a lower EPG count because of their lesser consumption of low stratum plants (<25 cm) and higher consumption of medium stratum plants (25–50 cm). The remaining studies were performed with experienced goats, which guarantee an appropriate "feed culture" acquisition [93]. Novelo-Chi et al. [68] used 12 animals to assess the effect of natural GIN infection in the macronutrient and CT intake. To do this, the authors observed the feeding behavior of the goats for two months. In the first month, all goats had a natural GIN infection and, after 30 days, the authors dewormed half of the group with a broad-spectrum commercial drug with a persistent effect of at least 28 days (moxidectin) [94]. The intake of macronutrients and CTs was not modified after deworming the animals when compared to the naturally infected animals. In addition, the EPG, packed cell volume, and live weight did not change during the experiment. In light of these results, the work of Torres-Fajardo et al. [70] evaluated GINs, CTs, and their interactions as modifiers of voluntary feed intake and selection in 32 goats. In this work, a group of animals was maintained free of GINs by means of a treatment with a broad-spectrum commercial persistent anthelmintic product, and polyethylene glycol (a neutralizing polymer) was used for CT removal. Independent of treatment, there were no changes in the goats' feeding behavior during the two-month trial, which was attributed to the resilience of local breeds [95], and the physiological and behavioral mechanisms that goats possess to counteract the apparently harmful effects of CTs [17,96–98]. In addition, the authors reported the consumption of 45 plant species and high selectivity towards gramineous plants. In the last work, Torres-Fajardo et al. [71]

emphasized the feeding pattern of goats in response to natural GIN infection. Then, the authors compared the pattern of voluntary feed intake of infected vs. dewormed goats, establishing two schedules (7:00–8:30 a.m. and 9:30–11:00 a.m.). There were no differences in the feeding behavior between the experimental groups during the month of observation. It is worth noting that all the goats significantly increased their grass intake during the late morning. Altogether, these findings support the hypothesis of the goats' resiliency and suggest the expression of behaviors with an aim to (i) balance the energy–protein ratio, (ii) avoid the saturation of detoxification pathways, (iii) avoid L_3 from grass in the early morning as a sign of "flight" behavior, and (iv) use PSCs from browsing in order to limit GIN establishment.

5. Final Remarks

If we consider that at least 260 plants could be used as feed resources for small ruminants in the low deciduous forest, but only 13 of them have been properly evaluated under a nutraceutical approach, it represents only 5% of such biodiversity. However, this percentage has implied two decades of research and endeavors from both researchers and collaborators. The brief summary of results presented regards the anthelmintic effect of plants and their extracts. Although it is one of the biologicals effects most studied during recent years, it must be noted that it is not the only response/effect that could be associated within the nutraceutical research area. Further research is needed to explore additional nutraceutical effects.

Native vegetation systems are inherently complex and relevant for domestic livestock worldwide, and researchers have a duty to understand the relationships between its biotic and abiotic components. In the present review, we gathered information from a vegetation system that has been used for centuries to sustain ruminant production. Further research should be intended to (i) evaluate the agronomic performance of potential nutraceutical plants, (ii) improve the methods for biomass estimation, (iii) focus on the ingestive behavior of ruminant species, (iv) standardize the techniques for PSC extraction and quantification, (v) evaluate the bioactivity of the whole range of PSC families, (vi) study the synergy/antagonism between PSCs, (viii) identify novel candidate molecules, (ix) increase the number of in vivo trials, and (x) establish communication channels with shepherds, farmers, extensionists, and professionals.

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