

Systematic Review

Effect of the Inclusion of Plant-Based Secondary Metabolites on Methane Production, Performance, and Fermentation Profile in Beef Cattle: A Meta-Analysis

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Simple Summary

Cattle production has adverse environmental impacts due to methane emissions generated during feed digestion, representing energy losses that could otherwise be allocated to growth. Consequently, secondary plant metabolites, such as tannins, flavonoids, terpenes, and phenolic compounds, have been examined in cattle diets to mitigate the methane emissions. This analysis aimed to evaluate whether terpenoids, essential oils, alkaloids, phenolic compounds, flavonoids, tannins, glycosides, and saponins can decrease methane production without impairing animal growth performance. A meta-analysis was performed on 43 scientific studies published in various databases. The findings demonstrated that tannins have the potential to reduce methane emissions and enhance energy availability in beef cattle without detrimentally affecting their growth. The observed effects are influenced by factors such as dosage, plant type, plant part used as an additive, and the dietary regimen of the animal. However, the effects of phenolic compounds, flavonoids, terpenes, and terpenoids are limited by the low number of published studies, high heterogeneity, and publication bias. Therefore, tannins may be a viable nutritional strategy for mitigating the environmental impacts associated with cattle production.



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Abstract

Rumen methane emissions contribute to global warming and energy loss in cattle. The use of plants rich in secondary metabolites to mitigate methane emissions has been extensively studied, with varying outcomes. The primary aim of this meta-analysis was to assess the impact of secondary metabolites on methane production, productive performance, and ruminal fermentation in beef cattle supplemented with plant-based additives. In accordance with the PRISMA guidelines, 43 of the 578 studies were selected for analysis, employing random-effects models to estimate the raw and standardized mean differences (RStudio: metafor and ggplot, with significance thresholds of $p \leq 0.05$ and $p \leq 0.1$). Heterogeneity was evaluated using the I^2 statistic, alongside a subgroup meta-regression examining

variables such as dose, additive type, additive form, and forage-to-concentrate ratio. After performing Egger's test and trim and fill analysis, it was determined that tannins reduced methane yield (g/kg DM, adjusted SDM = -0.463), increased propionate production (%), (RMD = 0.066 , $p = 0.001$), rumen pH (adjusted SMD = 0.307), and organic matter intake (RMD = 0.066 , $p = 0.01$). Despite phenolic compounds, flavonoids, terpenes, and terpenoids successfully modulating methane production, fermentative parameters, and nutrient intake, the limited number of comparisons and publication bias suggest caution in generalizing these results. In conclusion, supplementation with plant-based additives containing tannins offers a promising nutritional strategy for reducing enteric methane emissions while maintaining beef cattle performance.

Keywords: antimethanogenic effect; phenolic compounds; herbs; enteric methane; ruminants

1. Introduction

Beef cattle production plays a crucial economic and social role globally; however, it is also associated with significant environmental impact [1]. Methane (CH_4), a byproduct of ruminal microbial fermentation, is a major greenhouse gas that contributes to global warming [2]. Additionally, methane emissions represent an energy loss from the diet, estimated at 3–10% [3], which could otherwise support animal growth and metabolic efficiency of the animal. Thus, strategies aimed at reducing methane emissions not only address environmental concerns but may also improve nutrient utilization efficiency [4]. In recent years, considerable research has focused on identifying effective nutritional interventions to mitigate enteric methane emissions without adversely affecting the productivity of animals [5].

Among the potential mitigation strategies, plant-based additives have gained increasing attention because of their widespread availability, acceptance, and versatility across diverse animal production systems [6,7]. These additives are sources of secondary metabolites with diverse biological activities. The use of advanced analytical techniques has facilitated the identification and characterization of these compounds, enabling the correlation of specific chemical structures and biosynthetic pathways with their distinct biological effects [8]. Previously, secondary metabolites were considered toxic and antinutritional in animals; however, they have been shown to influence rumen ecology by modulating microbial interactions and fermentation pathways, particularly those that affect hydrogen utilization and methanogenic activity [9]. These changes can alter CH_4 production, fermentation profiles and nutrient utilization [3,9].

Specifically, plant-based products enriched with terpenoids, tannins, saponins, and flavonoids have been shown to affect methane emissions and parameters related to ruminal health and productivity [10]. For instance, legumes such as *Leucaena leucocephala* used as tannin sources have been shown to reduce methane when included at 30–35% of dry matter, while saponins and terpenoids have demonstrated efficacy through their impact on microbial community structure and archaeal metabolism, with reported methane reductions of up to 26% [9]. However, the response to supplementation is influenced by the specific metabolite type [11], plant source [12], basal diet composition, and production system context [13]. Consequently, compounds classified within the same chemical group may elicit variable effects across studies, contributing to the observed variability in the literature. The magnitude of these effects may further depend on factors such as the experimental duration, methane measurement methodology, and chemical diversity within each metabolite category [5,8,10].

Therefore, this meta-analysis aimed to evaluate the effects of secondary metabolites, administered as plant-based additives, on methane emissions, productive performance, and ruminal fermentation parameters in beef cattle.

2. Materials and Methods

2.1. Literature Search and Selection Criteria

This meta-analysis was conducted in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA 2020) guidelines (Figure 1) [14]. To evaluate the effects of plant-based secondary metabolites on methane emissions, productive performance, and ruminal fermentation in beef cattle, a systematic search was performed in the PubMed, Web of Science, Scopus, CAB Abstracts, and ScienceDirect databases. The last literature search will be conducted on December 1, 2025. The search strategy was formulated using the Population, Intervention, Comparison, and Outcome (PICO) terms: (“steers” OR “beef cattle” OR “cattle” OR “calf” OR “beef”) AND (“terpenoids” OR “essential oils” OR “alkaloids” OR “phenolic compounds” OR “flavonoids” OR “tannins” OR “glycosides” OR “saponins”) AND (“methane” OR “methane production” OR “CH₄”) AND (“in vivo”). The complete search strings are listed in Supplementary Table S1. Search terms were tailored to each database, and appropriate filters were applied as required. The classification of secondary metabolites was based on the frameworks established by Kabera et al. [8] and Li et al. [15]. Although flavonoids and tannins belong to the broad group of phenolic compounds, they were considered separate categories in this analysis because of their structural differences. Flavonoids are a subclass of polyphenols characterized by a basic C6-C3-C6 structure composed of two aromatic rings linked by a three-carbon chain. Tannins also belong to the polyphenol group but constitute a distinct class within non-flavonoid phenolic compounds and are therefore classified separately. Because polyphenols comprise a wide variety of compounds with different chemical characteristics, the separate classification of flavonoids and tannins allowed for the distinction of groups with specific structures within the general category of phenolic compounds [8].

In vivo studies involving beef cattle were included if they evaluated the dietary incorporation of secondary metabolites—including terpenoids, essential oils, alkaloids, phenolic compounds, flavonoids, tannins, glycosides, and saponins—through plant-based additives, and if they reported at least one of the following variables: methane production, productive performance, or ruminal fermentation profile. The studies considered must have provided sufficient data to estimate the effect size, including the mean, measure of dispersion, and number of replicates. Reviews, meta-analyses, and in vitro studies were excluded, as well as articles involving species outside of interest (e.g., humans, rodents, etc.) and those that did not contain the variables to be used [16].

The literature search, title and abstract selection, and full-text appraisal of the articles were performed independently by three researchers (K.M.V.-A., U.R.C.-M. and A.G.-T.) according to the eligibility criteria outlined above. All records retrieved from the databases were imported into EndNoteTM 20.6 (Build 17174) (Clarivate Analytics, Philadelphia, PA, USA) for reference management, duplicate removal, and study selection. Any disagreements during the title and abstract selection or full-text appraisal were resolved by consensus. The final eligibility decisions were reviewed and validated by two authors (M.E.T.-H and P.A.H.-G).

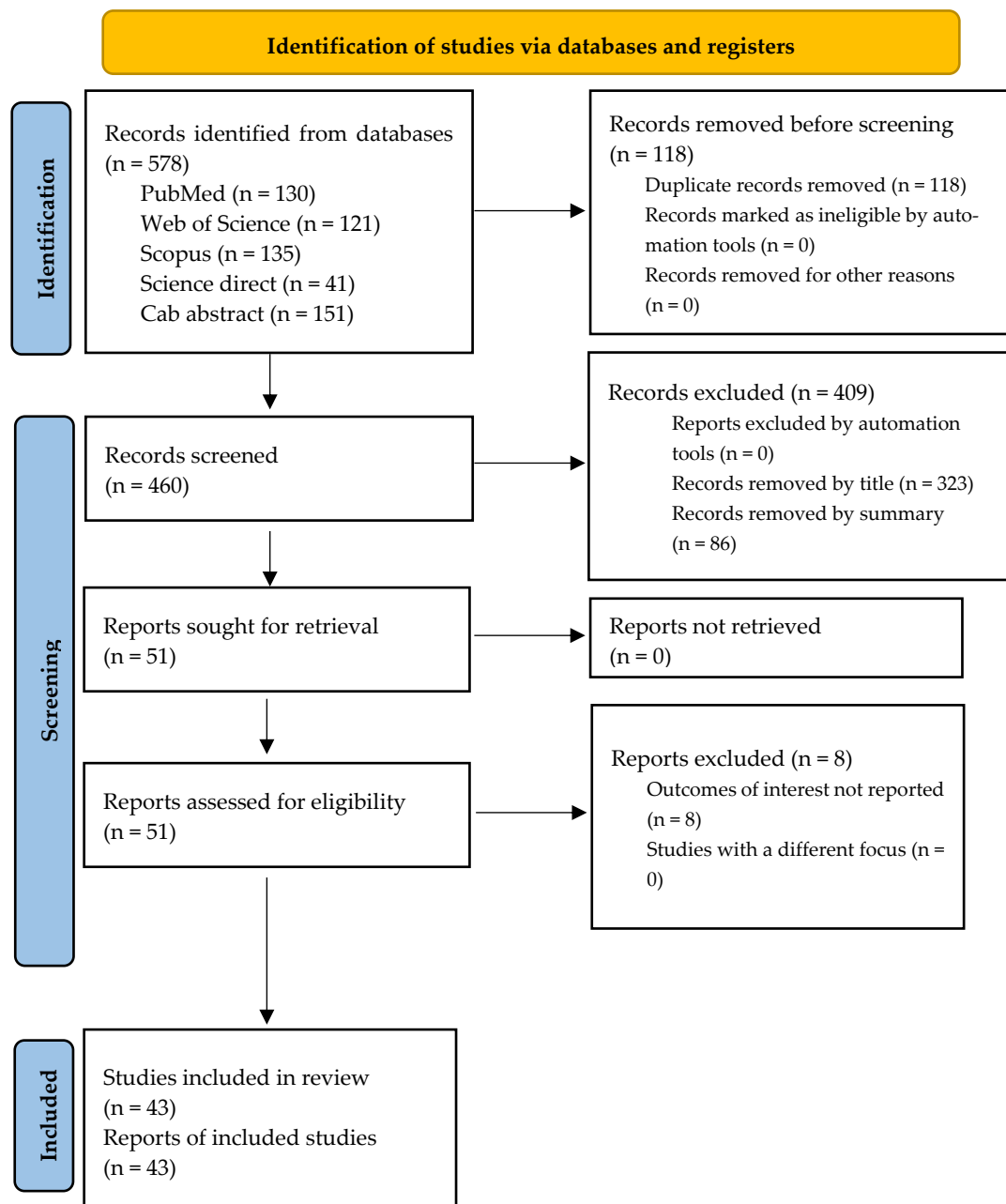


Figure 1. PRISMA flowchart for meta-analysis.

Once the final 43 studies were selected, data extraction was performed independently by two researchers (K.M.V.-A. and U.R.C.-M.) using a Microsoft Excel spreadsheet. The extracted data were checked by A.G.-T., and any discrepancies were resolved collectively. All data were extracted from the available tables, texts, or figures.

The supplementary activities carried out and the contributions of the other authors of the manuscript are described in the Author Contributions Section.

2.2. Data Extraction

Two authors working together extracted the following data from each study: sample size (n), means, standard deviation (SD), or standard error of the mean (SEM), type of secondary metabolite, form of the additive (extract, leaf, or oil), inclusion rate expressed in grams per kilogram of dry matter (where studies employed percentages of dry matter or milligrams per kilogram of dry matter as measurement units, relevant conversions were

executed), and characteristics of the diet (including the forage-to-concentrate ratio when explicitly reported). In instances where SD was not provided and SEM was documented, SD was calculated as follows: $SD = SEM \times \sqrt{n}$ [17].

When a study reported multiple treatments, each comparison with the control group was regarded as an independent unit to maintain consistency during data extraction.

2.3. Statistical Analysis

Data analysis was conducted in RStudio Desktop (version 2026.6.0.242, Posit Software, Boston, MA, USA) using the metafor (version 4.8.0) and ggplot2 (version 4.0.3) packages [18]. The nutritional composition of the diets was characterized using descriptive statistics, including the mean, minimum, maximum, standard deviation, and the coefficient of variation. Random-effects models were used to compare the control and treatment groups. Two measures were used to calculate the effect size: the crude mean difference (RMD, with biological interpretation of the original units of each variable), expressed in the original units of each variable and calculated as the direct difference between the treatment and control means, and the standardized mean difference (SMD, with comparisons between studies and with different scales or units), calculated using the Hedges method [19], which was applied when there were differences in scale or units between studies [20].

2.3.1. Publication Bias and Trim All Fill

Publication bias was assessed by visually reviewing the funnel plot and quantified using Egger's test [21]. A symmetrical funnel plot suggests the absence of publication bias, whereas asymmetry may indicate potential bias. A p -value ≤ 0.01 from Egger's test indicated that the funnel plot was asymmetrical and that potential publication bias existed. Subsequent sensitivity analyses were performed to ensure the reliability of the meta-analysis results, and Tweedie's non-parametric "trim and fill" procedure was implemented to determine whether additional randomly generated studies are required to reduce potential publication bias [22,23].

2.3.2. Meta-Regression

To investigate potential sources of heterogeneity, meta-regressions were performed using the method employed by DerSimonian and Larid [24], considering moderators selected a priori based on their biological plausibility, nutritional relevance, and availability in the extracted database. The moderators evaluated were the dose of the secondary metabolite or additive, expressed in g/kg DM, to explore possible responses dependent on the inclusion level; the type of additive or secondary metabolite, defined by the class and subclass of the supplemented compound; the form of the additive, including extract, leaf, oil, husk, flower, seed, bark, or shell, since these forms may differ in the availability and relative concentration of bioactive compounds; and the forage ratio, for example, 100:0, 95:5, or 80:20, due to its influence on the rumen environment, fermentation profile, and response of secondary metabolites in diets with different forage proportions. The reported results included the moderator coefficient (QM), p -value, τ^2 residual, and percentage of heterogeneity explained (R^2). The variables subjected to meta-regression were those exhibiting substantial heterogeneity ($I^2 > 60\%$) [25], and an additional meta-regression was performed to estimate the β coefficient, which delineates the direction and magnitude of the interaction between each response variable and specific moderators [18]. This study aimed to further elucidate the relationship between plant-based secondary metabolites and the form and source of the additive.

3. Results

3.1. Information Search

A total of 578 records were identified in the databases, of which 43 were included in the narrative review (Figure 1). After removing duplicates, 20.42% ($n = 118$) were excluded and 79.58% ($n = 460$) were retained for screening. During the title screening process, 323 records (55.88% of the total) were excluded, leaving 137 articles for abstract evaluation (23.70% of the total). Subsequently, 86 abstracts (14.88% of the total) were excluded for failing to meet the evaluation criteria, and 51 articles were reviewed in full (8.82% of the total). All full texts ($n = 51$) were retrieved for review. During the full-text review, eight studies (1.38% of the total) were excluded because they did not present data on methane measurements or productive performance. Ultimately, 7.44% of the total studies were included in the narrative synthesis (Figure 1).

The documents originated from studies conducted between 2018 and 2024 across various nations spanning three continents: the Americas, Asia, and Oceania. Brazil accounted for 30.2% of the studies, whereas Argentina and Peru together comprised only 4.6%. The geographical origins of all the included studies are presented in Table 1. Of the total number of animals examined, 37.2% were *Bos indicus*, followed by crossbred animals (34.8%). Additionally, 13.9% of the studies involved *Bos taurus* animals, 6.9% involved buffalo, and the remaining 6.9% comprised cattle of unspecified breed. Regarding the administered dosages, substantial variability was observed across studies, as well as in the methods of administration, with extracts accounting for 39.5%, leaves for 25.58%, and oils for 11.6% of the total articles (Table 1).

Table 1. Description of articles employed in the narrative review to identify metabolites utilized in beef cattle feed.

Author	Secondary Metabolite	Plant (Scientific Name)	Additive Presentation	Dosage	Country	Breed
Aboagye et al. [26]	Tannins	<i>Castanea</i> spp. and <i>Lysiloma divaricatum</i>	Extract	2.5, 15 g/kg DM	Canada	Crossbreeds
Aboagye et al. [5]	Tannins	<i>Castanea</i> spp.	Extract	15, 15, 20 g/kg DM	Canada	Crossbreeds
Alecrim et al. [27]	Tannins	<i>Lotus uliginosus</i> <i>Lotus angustissimus</i>	Leaf	4, 12 g/kg DM	Uruguay	Hereford
Alemu et al. [28]	Terpenoids	Carvacrol *	Oil	0.15 g/kg DM	Canada	Crossbreeds
Ampapon et al. [29]	Tannins and saponins	<i>Garcinia mangostana</i> , <i>Musa paradisiaca</i> L.	Peel, flower	167, 113, 145 g/kg DM	Thailand	Buffalo
Ampapon et al. [30]	Tannins and saponins	<i>Nephelium lappaceum</i>	Peel	20, 40, 60 g/kg DM	Thailand	Brahman × Thai Native
Benetel et al. [31]	Phenols	<i>Origanum vulgare</i>	Oil	3 mL/kg DM	Brazil	Nellore
Bharanidharan et al. [4]	Flavonoids	<i>Ipomoea nil</i> L.	Seed	50 g/kg DM	South Korea	Hanwoo
Bitsie et al. [32]	Flavonoids	<i>Allium sativum</i> and <i>Citrus aurantium</i>	Extract	2.5 g/kg DM	United States	Angus × Simmental
Caetano et al. [33]	Tannins	<i>Vitis vinifera</i> L.	Solid residue	31.2 g/kg DM	Australia	Angus

Table 1. Cont.

Author	Secondary Metabolite	Plant (Scientific Name)	Additive Presentation	Dosage	Country	Breed
Cidrini et al. [34]	Tannins	<i>Schinopsis lorentzii</i> and <i>Castanea</i> spp.	Extract	7 g/kg DM	Brazil	Nellore
Coneglian et al. [35]	Terpenes	<i>Anacardium occidentale</i> and <i>Ricinus communis</i>	Oil	1, 2, 4, 8 g/kg DM	Brazil	Nellore
Cuervo et al. [36]	Tannins and saponins	<i>Anacardium occidentale</i>	Extract	0.4 g/kg DM	United States	Angus crossbred
de Sa Assis et al. [37]	Tannins	<i>Anadenanthera macrocarpa</i> , <i>Mimosa tenuiflora</i> , <i>Prosopis juliflora</i>	Extract	10, 10, 10 g/kg DM	Brazil	Nellore
Fagundes et al. [38]	Tannins	<i>Acacia mimos</i>	Extract	12.5, 25 g/kg DM	Brazil	Nellore
Fonseca et al. [39]	Tannins	<i>Arachis hypogaea</i> , <i>Sorghum</i> spp., <i>Glycine max</i>	Husk, kernel, husk	950, 950, 950 g/kg DM	Brazil	Nellore
González et al. [40]	Tannins	<i>Lotus tenuis</i>	Leaf	0.21, 0.48 g/kg DM	Argentina	Angus
Jiménez-Ocampo et al. [41]	Monoterpenes	<i>Citrus sinensis</i> L.	Oil	2.5, 5.0 g/kg DM	Mexico	<i>Bos indicus</i> × <i>Bos taurus</i>
Khejornsart et al. [42]	Tannins	<i>Piper sarmentosum</i> , <i>Cymbopogon citratus</i> , <i>Anacardium occidentale</i> L., <i>Careya arborea</i> Roxb	Leaf	1.66, 1.63, 1.67, 1.66 g/kg DM	Thailand	Thai Native × Brahman × Charolais
Koenig et al. [43]	Tannins	<i>Acacia mearnsii</i>	Extract	25 g/kg DM	Canada	Heifers
Kumari et al. [44]	Tannins and Saponins	<i>Trigonella foenum-graecum</i> L.	Seed	120.04 g/kg DM	India	Murrah Buffaloes
Magnani et al. [45]	Tannins	<i>Castanea</i> spp. and <i>Lysiloma divaricatum</i>	Extract	0.7 g/kg DM	Brazil	Nellore
Mezzomo et al. [46]	Tannins	<i>Castanea</i> spp. and <i>Lysiloma divaricatum</i>	Extract	25 g/kg DM	Brazil	Nellore
Molina-Botero et al. [47]	Phenols	<i>Enterolobium cyclocarpum</i> a <i>Gliricidia sepium</i>	Leaf	150 g/kg DM	Mexico	<i>Bos taurus</i> × <i>Bos indicus</i>
Moscoso et al. [48]	Tannins	<i>Castanea</i> spp.	Extract	10, 20 g/kg DM	Peru	Brown Swiss × crossbreeds o
Norris et al. [49]	Tannins	<i>Lysiloma divaricatum</i>	Extract	15, 30, 45 g/kg DM	United States	British crossbreeds
Okedoyin et al. [50]	Terpenoids	<i>Pimpinella anisum</i> , <i>Syzygium aromaticum</i> , <i>Origanum vulgare</i> , <i>Mentha piperita</i> L.	Oil	4 mL/d	United States	Black Angus
Pena-Bermudez et al. [51]	Phenolic compounds	<i>Ilex paraguariensis</i>	Extract	5, 10, 20 g/kg DM	Brazil	Nellore
Perna Junior et al. [52]	Tannins	<i>Acacia mearnsii</i>	Extract	5, 10, 15 g/kg DM	Brazil	Nellore
Phesatcha et al. [53]	Tannins	<i>Flemingia macrophylla</i>	Flour	49, 52, 53 g/kg DM	Thailand	Thai Native

Table 1. Cont.

Author	Secondary Metabolite	Plant (Scientific Name)	Additive Presentation	Dosage	Country	Breed
Poornachandra et al. [54]	Tannins and saponins	<i>Tamarindus indica</i> , <i>Sapindus mukorossi</i> , mixture	Bark, extract	7.1, 4.3 g/kg DM	India	Holstein Friesian × Hallikar
Silva et al. [55]	Tannins	<i>Acacia mearnsii</i>	Extract	8, 16, 32 g/kg DM	Brazil	Nellore
Somma et al. [56]	Flavonoids	<i>Alternanthera sissoo</i>	Leaf	20, 40, 60, 80 g/kg DM	Thailand	Thai Native
Stewart et al. [57]	Tannins	<i>Lotus corniculatus</i> L., <i>Onobrychis viciifolia</i> Scop., <i>Sanguisorba minor</i>	Leaf	0.2, 0.2, 0.1, 0.6, 2.5, 4.5 g/kg DM	United States	Angus
Stifkens et al. [58]	Tannins	<i>Leucaena leucocephala</i>	Leaf	180, 360, 480 g/kg DM	Australia	Droughtmaster
Teobaldo et al. [59]	Tannins	<i>Vitis vinifera</i> L.	Berries	1.5 g/kg DM	Brazil	Nellore
Tseu et al. [60]	Tannins	<i>Acacia mearnsii</i>	Bark	7.5, 15, 22.5	Brazil	Nellore
van Cleef et al. [61]	Tannins	<i>Sericea lespedeza</i>	Leaf	9.5, 36.3, 59.7, 82.3 g/kg DM	United States	Angus crossbreed
Vazquez-Carrillo et al. [62]	Tannins	<i>Cosmos bipinnatus</i> , <i>Matricaria chamomilla</i> , <i>Cymbopogon citratus</i>	Leaf	365, 365; 100, 280, 411, 572 g/kg DM	Mexico	Charolais × Brown Swiss
Viennasay and Wanapat [63]	Tannins and saponins	<i>Flemingia macrophylla</i>	Leaf	200, 400, 600 g/kg DM	Thailand	Crossbreeds
Wanapat et al. [64]	Tannins	<i>Musa paradisiaca</i> L.	Flower	29.4, 56.0 g/kg DM	Thailand	Buffalo
Wanapat et al. [65]	Phenolic compounds	<i>Musa paradisiaca</i> L., <i>Carica papaya</i> , <i>Ananas comosus</i> , <i>Citrus sinensis</i>	Peel	150 g/kg DM	Thailand	Steers
Wann et al. [66]	Phenolic compounds	<i>Tiliacora triandra</i>	Leaf	28.96, 19.94, 10.31 g/kg DM	Thailand	Thai Native

* In this study, a commercial mixture of cinnamaldehyde essential oil was used without mentioning the extraction plant. Phenolic compounds: non-flavonoid and non-tannin phenolics, or compounds reported as a general category.

The analyzed articles highlighted the utilization of six categories of secondary metabolites, with tannins emerging as the most frequently reported, present in 58.14% of the reviewed publications. This was followed by the combined occurrence of tannins and saponins, which accounted for 13.95% of the total. Only 11.63% of articles defined the inclusion of phenolic compounds or phenols without referring to the type of metabolite used. Monoterpenes, terpenes, and terpenoids were reported in 9.3% of the studies, whereas phenols and flavonoids were reported in 6.98% of the studies (Table 1).

3.2. Diet Composition

The diets employed in the studies analyzed for the narrative synthesis exhibited substantial variability (Table 2). The dry matter content ranged from 344 to 963 g/kg, with a coefficient of variation (CV) of 28%. The fiber fractions demonstrated considerable ranges: neutral detergent fiber (NDF) ranged from 61.8 to 747 g/kg and acid detergent fiber (ADF) ranged from 20.0 to 741 g/kg, both with high coefficients of variation (39–53%), indicating diets with varying forage-to-concentrate ratios. Similarly, the ether extract and starch content displayed significant variability, with CVs of 79% and 94%, respectively. The

mean ether extract concentration in the ruminant diets was 3.59%, whereas the average starch inclusion was 17.27%. These parameters are closely associated with alterations in ruminal fermentation. The inclusion of secondary metabolites was markedly heterogeneous and asymmetric. For instance, tannins had a mean of 17.3 g/kg of dry matter, with a maximum of 167 g/kg, and exhibited a wide distribution (skewness = 3.09), reflecting a pattern characterized by multiple low-dose comparisons and a limited number of high-dose studies.

Table 2. Descriptive statistics of diets (dry matter basis) incorporating secondary metabolites in beef cattle.

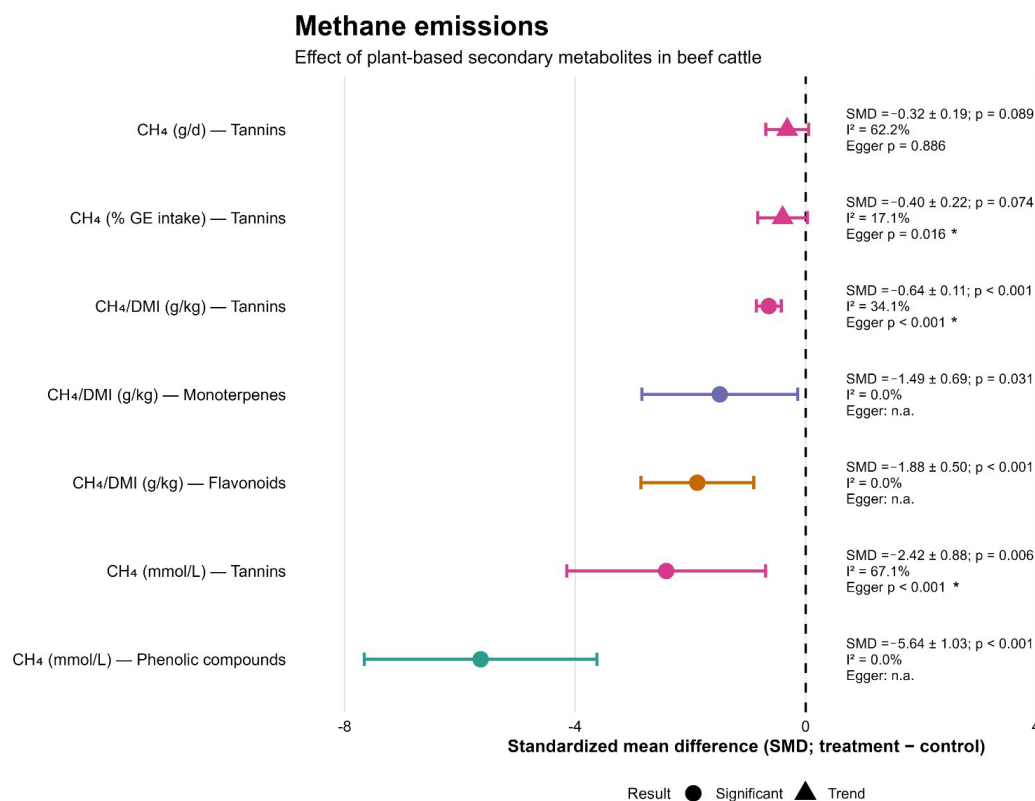
Variable	n	Mean	Min	Max	SD	SE	CV	Skewness	Kurtosis
DM, g/kg	90	719.40	344	963.4	201.8	21.27	28.05	−0.49	−1.28
OM, g/kg	72	911.81	737	973.0	43.07	5.080	4.720	−1.69	3.52
CP, g/kg	120	139.07	9.70	287.0	39.64	3.620	28.51	0.31	2.90
NDF, g/kg	122	410.72	61.8	747.0	160.9	14.57	39.19	0.17	−0.81
ADF, g/kg	93	262.74	20.0	741.0	139.3	14.44	53.01	0.20	0.05
EE, g/kg	47	35.91	3.56	176.0	28.36	4.140	78.95	2.69	10.31
Starch, g/kg	27	172.75	4.00	524.0	162.7	31.31	94.17	0.66	−0.99
Ash, g/kg	46	287.38	6.16	771.0	299.5	44.16	104.2	0.68	−1.45
GE, Mcal/kg	43	4.32	3.58	5.39	0.495	0.075	11.5	0.58	0.29
NEg, Mcal/kg	23	1.03	0.76	1.260	0.210	0.040	20.00	−0.17	−1.89
Tannins, g/kg	84	17.32	0	167.0	29.50	3.220	170.4	3.09	10.85
Terpenes, g/kg	5	3.00	0	8.000	3.160	1.410	105.4	0.57	−1.55
Terpenoids, g/kg	8	0.27	0	0.400	0.190	0.070	69.57	−0.56	−1.76
Saponins, g/kg	12	1.73	0	6.300	2.290	0.660	132.9	0.85	−0.97
Phenolic compounds, g/kg	7	13.46	0	28.96	10.00	3.780	74.28	0.17	−1.58
Phenols, g/kg	5	42.00	0	150.0	62.21	27.82	148.1	0.92	−1.10
Flavonoids, g/kg	8	7.19	0	50.00	17.34	6.130	241.3	1.84	1.66
Tannins + saponins, g/kg	4	0.20	0	0.400	0.230	0.120	115.5	0.00	−2.44
Monoterpenes, g/kg	3	2.50	0	5.000	2.500	1.440	100.0	0.00	−2.33

DM: Dry matter; OM: Organic matter; CP: Crude protein; NDF: Neutral detergent fiber; ADF: Acid detergent fiber; EE: Ether extract; NEg: Net energy for gain; GE: Gross energy; n: Number of comparisons; Mean: Average; Min: Minimum; Max: Maximum; SD: Standard deviation; SE: Standard error; CV: Coefficient of variation; Phenolic compounds: non-flavonoid and non-tannin phenolics, or compounds reported as a general category; Skewness and Kurtosis: These represent the degree of skewness and distribution around their means, respectively.

3.3. Comparison in Subgroups of the Effect of Secondary Metabolites on Methane Emissions, Rumen Fermentation, and Animal Production

3.3.1. Effect of Secondary Metabolites on Methane Production

Based on the reference literature, the random-effects model by subclass showed that the inclusion of tannins via plant-based additives in the diet of beef cattle tended ($p = 0.089$) to reduce methane production (g/d, SMD = -0.32 , $I^2 = 62.2\%$, and Egger $p = 0.886$). Despite the superior anti-methanogenic efficacy of flavonoids and monoterpenes over tannins (CH_4/DMI , g/kg; SMD = -1.88% and -1.49 versus -0.64 , respectively; $p \leq 0.05$) (Figure 2), the former two had a significant and homogeneous effect, but with a small number of comparisons ($n < 10$), as is also the case for phenolic compounds. In tannins, the sensitivity analysis (Supplementary Figure S1) showed that the reducing effect on CH_4 expressed as energy losses (% GE intake) and molar concentration (mmol/L) depended on publication bias rather than the inclusion of secondary metabolites, with the exception of CH_4 yield (g/kg DMI), where the anti-methanogenic effect of tannins was consistent (SMD = -0.463 , CI 95% 0.688 to -0.238) [$n = 8$]. The trim and fill analysis is reported in Supplementary Figure S2.



Negative values indicate lower methane emissions relative to the control group.
I² and Egger's test were reported for each comparison set when applicable.

Figure 2. The forest plot illustrates the impact of plant-based secondary metabolites on methane emissions in beef cattle. Phenolic compounds: non-flavonoid and non-tannin phenolics, or compounds reported as a general category. The analysis employed a random-effects model for each metabolite subclass, considering only outcomes with $p \leq 0.10$; SMD: standardized mean difference. * Trim and fill effect size SMD (95% CI) [n = imputed studies]: CH₄ (% GE intake)—Tannins = -0.046 (-0.528 to 0.436) [n = 4], CH₄/DMI (g/kg)—Tannins = -0.463 (-0.688 to -0.238) [n = 8], CH₄ (mmol/L)—Tannins = -0.617 (-2.855 to 1.620) [n = 4].

3.3.2. Effect of Secondary Metabolites on Fermentation Parameters

The incorporation of tannins into the diets of beef cattle modulated ruminal fermentation towards greater propionate production (adjusted SMD = 0.307, 95% CI 0.088 to 0.527 [n = 6]), but showed no significant effects on acetate production (adjusted SMD = 0.196, 95% CI -0.018 to 0.411 [n = 9]) and acetate:propionate ratio (adjusted SMD = -0.204 , 95% CI 0.453 to 0.046 [n = 9]) after adjusting the SMDs for publication bias (Table 3). The effects of propionate (RMD = 24.96 and SMD = 2.501, $p \leq 0.001$) and butyrate (SMD = 5.526, $p \leq 0.001$) were similar for terpenes but not for terpenoids, which decreased ruminal fermentation by reducing total VFA production (RMD = 4.3, $p = 0.03$). However, even with low heterogeneity, the risk of publication bias was not assessed because of the small number of comparisons; therefore, caution should be exercised when generalizing these findings.

The effect of tannin inclusion on pH (RMD = 0.047, $p = 0.066$, Egger $p = 0.288$) indicates alkalization of the ruminal environment. For terpenoids, the consistency between results ($I^2 = 0\%$) suggests a higher pH (RMD = 0.106, $p = 0.03$ and SMD = 0.516), which would be related to a lower fermentation rate and a higher NH₃-N concentration. However, publication bias cannot be ruled out as a cause of these terpenoid-mediated effects. Phenolic compounds (heterogeneity > 90%, without Egger test) seemed to promote total VFA production (mmol/L) with a lower production of acetate (RMD = -2.426 , $p = 0.034$) and butyrate (RMD = -0.648 and SMD = -1.42 , $p \leq 0.05$), and a higher production of propionate (RMD = 3.135 and SMD = 2.599, $p < 0.001$). With less heterogeneity ($I^2 < 35\%$) but

without assessing the risk of publication bias, both phenolic compounds (RMD = -0.761 and SMD = -2.47 , $p < 0.001$) and tannins (RMD = -80.13 and SMD = -1.5 , $p < 0.001$) showed defaunation capacity by reducing protozoan populations.

3.3.3. Effect of Secondary Metabolites on Animal Production

In this subgroup analysis (Table 4), supplementation with plant-based secondary metabolites had no significant effect on productive performance ($p > 0.05$). Regarding nutrient intake and based on the referenced articles, tannins promoted OM intake (kg DM/d, RMD = 0.066 , $p = 0.01$, Egger $p = 0.653$), but reduced GE intake (Mcal/d). This response in energy intake persisted (adjusted SMD = -0.146 CI 95% -0.24 to -0.052 [$n = 2$]) after the trim and fill analysis.

The adjustment for publication bias indicated that the observed effect of tannins on increasing DM, CP, NDF, and ADF intake was not significant after the trim-and-fill analysis. Flavonoids had a significant effect on nutrient intake, characterized by lower dry matter intake (SMD = -0.348), associated with a reduction in the consumption of NDF (SMD = -0.272) and ADF (SMD = -0.153), and an increase in GE intake (RMD = 1.939). In contrast, phenolic compounds promoted the intake of OM (SMD = 1.966), CP (SMD = 1.019), and fiber fractions (SMD > 0.6). However, despite their significance ($p < 0.05$), high homogeneity ($I^2 < 50\%$), and a low number of comparisons for these response variables ($n < 10$), they should be considered.

3.4. Meta-Regression Analysis

The meta-regression analysis (Table 5) elucidates the moderators that influence the measured variables and their effects. Methane (CH₄) production, expressed in mmol/L and grams per day (g/d), was significantly influenced ($p \leq 0.05$) by the plant-based additive utilized. Additionally, for CH₄ production expressed in g/d, a statistically significant effect was observed concerning the plant part utilized. However, low or negative R² values indicate considerable heterogeneity.

The analysis of the β coefficient (Table 6) indicated that the inclusion of banana flowers had the most significant reducing effect on CH₄ production (mmol/L, $p < 0.001$), implying a direct influence on ruminal fermentation and hydrogen availability. Conversely, *Acacia mimos*a and chestnut wood, evaluated as extracts, demonstrated substantial reductions (SMD = -2.56 and SMD = -2.521 , respectively) in CH₄ production (g/d; $p \leq 0.05$) relative to the control, suggesting an overall effect on the animals. In terms of nitrogen metabolism, the concentration of NH₃-N (mg/dL) markedly decreased following the administration of *Anacardium occidentale* L. and *Cymbopogon citratus* ($p = 0.008$), indicating reduced ruminal protein degradation. Conversely, the inclusion of banana flowers elevated NH₃-N concentration ($p < 0.001$), which may be associated with the stabilization of ruminal pH.

Table 3. Comparison across subgroups of the effect of secondary metabolites on fermentation variables in beef cattle.

Variable	Metabolite	k RMD/SMD	Effect Size Estimates				Heterogeneity Tests		Publication Bias	
			RMD	<i>p</i> -Value	SMD	<i>p</i> -Value	RMD I ² (%)	SMD I ² (%)	Egger <i>p</i>	Trim and Fill Effect Size SMD (95% CI) [n = Imputed Studies]
Acetate (%)	Phenolic compounds	7	−2.426	0.034	−1.870	0.058	98.7	89.3	-	-
	Tannins	23	−1.669	0.074	−0.010	0.917	92.2	5.60	<0.001	0.196 (−0.018 to 0.411) [n = 9]
Propionate (%)	Phenolic compounds	7	3.135	<0.001	2.599	<0.001	96.4	48.2	-	-
	Tannins	23	1.915	0.005	0.457	<0.001	97.2	0	<0.001	0.307 (0.088 to 0.527) [n = 6]
	Terpenes	4	24.960	<0.001	2.501	<0.001	0	0	-	-
Butyrate (%)	Phenolic compounds	7	−0.648	0.012	−1.420	0.033	85.4	79.5	-	-
	Terpenes	4	16.110	<0.001	5.526	<0.001	61.5	0	-	-
Acetate: propionate	Phenolic compounds	7	−0.477	<0.001	−2.080	<0.001	93.1	35.1	-	-
	Tannins	26	−0.229	<0.001	−0.450	<0.001	59.2	9.20	0.004	−0.204 (−0.453 to 0.046) [n = 9]
Total VFA (mmol/L)	Phenolic compounds	4	4.620	<0.001	0.914	0.018	0	0	-	-
	Terpenoids	5	−4.300	0.049	−0.450	0.090	0	0	-	-
Ruminal pH	Tannins	32	0.047	0.066	0.130	0.211	63.0	0	0.288	-
	Terpenoids	5	0.106	0.030	0.516	0.050	0	0	-	-
NH ₃ -N (mg/dL)	Terpenoids	5	2.080	<0.001	1.265	0.001	62.5	42.2	-	-
Protozoa (×10 ⁵ /mL)	Phenolic compounds	4	−0.761	<0.001	−2.470	<0.001	34.8	0	-	-
Total Protozoa (×10 ³ /mL)	Tannins	6	−80.130	<0.001	−1.500	<0.001	0	30.1	-	-

VFA: Volatile fatty acids; Phenolic compounds: non-flavonoid and non-tannin phenolics, or compounds reported as a general category; RMD: raw mean difference and its associated 95% confidence interval; SMD: standardized mean difference and its associated 95% confidence interval; I²: percentage of variation, k: number of comparisons (treatment vs. control); k RMD and k SMD: The number of comparisons for RMD and SMD was the same for both media differences.

Table 4. Comparative analysis of the influence of secondary metabolites on production variables across different subgroups of beef cattle.

Variable	Metabolite	k RMD/SMD	Effect Size Estimates				Heterogeneity Tests (%)		Publication Bias	
			RMD	<i>p</i> -Value	SMD	<i>p</i> -Value	RMD I ²	SMD I ²	Egger <i>p</i>	Trim and Fill Effect Size SMD (95% CI) [n = Imputed Studies]
Productive performance										
Final Body Weight (kg)	Flavonoids	3	−4.1	0.350	−0.152	0.362	0	0	-	-
	Tannins	11	−3.334	0.299	−0.161	0.377	52.9	37.9	0.152	-
ADG (kg/d)	Tannins	21	−0.023	0.446	−0.01	0.922	75.6	0	0.073	−0.017 (−0.187 to 0.152) [n = 1]
	Flavonoids	3	−0.067	0.181	−0.218	0.193	0	0	-	-
Gain: feed	Flavonoids	6	−0.001	0.659	−0.035	0.768	20	0	-	-
	Tannins	9	0.002	0.418	0.19	0.182	3.9	0	-	-
Nutrient intake (Dry matter basis, kg/d)										
DM	Phenolic compounds	10	0.484	<0.001	1.798	0.004	87.7	80.4	<0.001	0.988 (−0.289 to 2.265) [n = 7]
	Phenols	3	−0.117	<0.001	−0.654	0.435	0.1	76.8	-	-
	Flavonoids	9	−0.348	0.013	−0.272	0.005	10.2	0	-	-
	Tannins	73	0.336	0.01	0.09	0.164	96.2	12.9	<0.001	0.048 (−0.062 to 0.157) [n = 3]
	Terpenes	4	0.322	0.631	0.137	0.666	0	0	-	-
OM	Phenolic compounds	3	0.367	<0.001	1.966	<0.001	0	0	-	-
	Tannins	23	0.066	0.01	0.111	0.383	1.7	0	0.653	-
CP	Phenolic compounds	6	0.066	<0.001	1.019	<0.001	0	0	-	-
	Flavonoids	3	−0.03	0.756	−0.051	0.76	0	0	-	-
	Tannins	26	0.002	<0.001	0.291	0.095	0	37.5	<0.001	0.315 (−0.021 to 0.652) [n = 2]
	Terpenes	4	0.05	0.677	0.118	0.709	0	0	-	-
NDF	Phenolic compounds	6	0.141	0.007	0.613	0.024	32.3	0	-	-
	Flavonoids	3	−0.277	0.024	−0.369	0.028	0	0	-	-
	Tannins	25	0.166	0.09	−0.013	0.919	94.4	0	0.031	−0.013 (−0.327 to 0.171) [n = 0]
	Terpenes	4	0.065	0.689	0.113	0.721	0	0	-	-
ADF	Phenolic compounds	6	0.114	0.008	0.748	0.007	64	0	-	-
	Flavonoids	3	−0.153	0.037	−0.341	0.042	0	0	-	-
	Tannins	18	0.162	0.112	−0.055	0.725	98.6	0	0.006	−0.055 (−0.460 to 0.153) [n = 0]

Table 4. Cont.

Variable	Metabolite	k RMD/SMD	Effect Size Estimates				Heterogeneity Tests (%)		Publication Bias	
			RMD	<i>p</i> -Value	SMD	<i>p</i> -Value	RMD I ²	SMD I ²	Egger <i>p</i>	Trim and Fill Effect Size SMD (95% CI) [n = Imputed Studies]
EE	Phenolic compounds	3	0.017	0.799	0.078	0.814	0	0	-	-
	Tannins	7	0.053	0.27	0.366	0.259	77.2	48	-	-
	Terpenes	4	0.012	0.556	0.168	0.596	0	0	-	-
GE (Mcal/d)	Flavonoids	3	1.939	0.08	0.521	0.127	0	0	-	-
	Monoterpenes	2	0.09	0.994	0.004	0.995	0	0	-	-
	Tannins	13	−1.982	0.059	−0.147	0.414	10.5	0	0.081	−0.146 (−0.240 to −0.052) [n = 2]
ME (Mcal/d)	Tannins	6	−0.218	0.356	−0.249	0.295	0	0	-	-

ADG: average daily gain; DM: dry matter; OM: organic matter; CP: crude protein; NDF: neutral detergent fiber; ADF: acid detergent fiber; EE: ether extract; GE: gross energy; ME: metabolizable energy; Phenolic compounds: non-flavonoid and non-tannin phenolics, or compounds reported as a general category; RMD: raw mean difference and its associated 95% confidence interval; SMD: standardized mean difference and its associated 95% confidence interval; I²: percentage of variation; k: number of comparisons (treatment vs. control); k RMD and k SMD: The number of comparisons for RMD and SMD was the same for both media differences.

Table 5. Meta-regression of the effect of secondary metabolites on fermentation variables in beef cattle.

Variable	Moderator	QM	p-Value	R ²	Tau ²
CH ₄ (mmol/L)	Dosage	2.02	0.16	14.71	5.410
	Additive	66.05	<0.001	>99.9	<0.001
	Additive form	3.80	0.15	6.10	5.950
	Forage: concentrate	3.47	0.18	6.91	5.900
CH ₄ (g/d)	Dosage	0.24	0.62	0.00	0.650
	Additive	46.83	0.01	0.00	0.610
	Additive form	25.75	<0.001	23.24	0.460
	Forage: concentrate	28.76	<0.001	12.49	0.530
Total VFA (mmol/L)	Dosage	14.54	<0.001	77.98	0.090
	Additive	65.28	<0.001	>99.9	<0.001
	Additive form	39.14	<0.001	80.18	0.080
	Forage: concentrate	42.68	<0.001	>99.9	<0.001
NH ₃ -N (mg/dL)	Dosage	2.66	0.10	1.90	3.900
	Additive	144.50	<0.001	93.38	0.260
	Additive form	34.23	<0.001	0.00	4.250
	Forage: concentrate	47.92	<0.001	67.01	1.310
Protozoa (×10 ⁵ /mL)	Dosage	1.88	0.17	0.00	10.44
	Additive	18.88	0.03	32.72	6.520
	Additive form	17.90	<0.001	55.47	4.320
	Forage: concentrate	14.94	<0.001	48.34	5.010

VFA: volatile fatty acids; QM: moderator coefficient, is considered statistically significant at the $p \leq 0.05$; R²: degree of heterogeneity; Tau²: between-study variance.

Table 6. Meta-regression presenting beta coefficients for the influence of secondary metabolites on fermentation parameters in beef cattle.

Variable	Moderator	Author	Additive Description	Dosage	ß	p-Value
CH ₄ (mmol/L)	Dose				−0.006	0.011
	Additive (<i>Musa paradisiaca</i> L.)	Wanapat et al. [64]	Flower	29.4, 56.0 g/kg DM	−8.558	<0.001
CH ₄ (g/d)	Additive (<i>Acacia mimos</i> a)	Fagundes et al. [38]	Extract	12.5, 25 g/kg DM	−2.560	0.006
	Additive (<i>Cymbopogon citratus</i>)	Khejornsart et al. [42]	Leaf	1.66, 1.63, 1.67, 1.66 g/kg DM	−1.878	0.035
		Vazquez-Carrillo et al. [62]		100, 280, 365, 411, 572 g/kg DM		
	Additive (<i>Leucaena leucocephala</i>)	Stifkens et al. [58]	Leaf	180, 360, 480 g/kg DM	2.770	0.003
	Additive (<i>Lotus tenuis</i>)	González et al. [40]	Leaf	0.21, 0.48 g/kg DM	−1.659	0.011
	Additive (<i>Madera Castanea</i> spp.)	Moscoso et al. [48]	Extract	10, 20 g/kg DM	−2.521	0.001
	Additive (<i>Vitis vinifera</i> L.)	Caetano et al. [33]	Solid residue	31.2 g/kg DM	−1.626	0.076
	Additive (<i>Pharbitis nil</i>)	Bharanidharan et al. [4]	Seed	50.0 g/kg DM	−1.570	0.088
	Additive (<i>Sanguisorba minor</i>)	Stewart et al. [57]	Leaf	0.2, 0.2, 0.1, 0.6, 2.5, 4.5 g/kg DM	−1.348	0.035
	Additive (<i>Castanea</i> spp. and <i>Lysiloma divaricatum</i>)	Magnani et al. [45]	Extract	0.70 g/kg DM	−1.752	0.059
		Mezzomo et al. [46]		25.0 g/kg DM		
	Additive form (<i>Acacia mearnsii</i>)	Tseu et al. [60]	Bark	7.5, 15, 22.5 g/kg DM	−5.200	<0.001

Table 6. Cont.

Variable	Moderator	Author	Additive Description	Dosage	ß	p-Value
Total VFA (mmol/L)	Dose				0.003	0.060
	Additive (<i>Musa paradisiaca</i> L.)	Wanapat et al. [64]	Flower	29.4, 56.0 g/kg DM	6.485	<0.001
	Additive (<i>Lysiloma divaricatum</i>)	Norris et al. [49]	Extract	15, 30, 45 g/kg DM	1.360	0.062
	Additive (<i>Tiliacora triandra</i>)	Wann et al. [66]	Leaf	28.96, 19.94, 10.31 g/kg DM	2.110	0.009
NH ₃ -N (mg/dL)	Unit (mL/d)	Benetel et al. [31]	Oregano essential oil	3.0 mL/kg DM	2.838	<0.001
		Okedoyin et al. [50]	Anise, clove, oregano, mint	4.0 mL/d		
	Additive (<i>Anacardium occidentale</i> L.)	Khejornsart et al. [42]	Leaf	1.66, 1.63, 1.67 and 1.66 g/kg DM	−4.621	0.008
	Additive (<i>Anacardium occidentale</i> and <i>Ricinus communis</i>)	Coneglian et al. [35]	Oil	1, 2, 4, 8 g/kg DM	1.568	0.030
	Additive (<i>Cymbopogon citratus</i>)	Khejornsart et al. [42]	Leaf	1.66, 1.63, 1.67, 1.66 g/kg DM	−4.528	0.008
		Vazquez-Carrillo et al. [62]		100, 280, 365, 411, 572 g/kg DM		
	Additive (<i>Careya arborea</i>)	Khejornsart et al. [42]	Leaf	1.66, 1.63, 1.67, 1.66 g/kg DM	−7.948	0.001
	Additive (<i>Leucaena leucocephala</i>)	Stifkens et al. [58]	Leaf	180, 360, 480 g/kg DM	3.822	0.072
	Additive (<i>Musa paradisiaca</i> L.)	Wanapat et al. [64]	Flower	29.4, 56.0 g/kg DM	41.48	<0.001
	Additive (<i>Schinopsis lorentzii</i> and <i>Castanea</i> spp.)	Cidrini et al. [34]	Extract	7.0 g/kg DM	1.914	0.048
Protozoa (×10 ⁵ /mL)	Additive (<i>Tiliacora triandra</i>)	Wann et al. [66]	Leaf	28.96, 19.94, 10.31 g/kg DM	3.001	0.001
	Additive (<i>Musa paradisiaca</i> L., <i>Carica papaya</i> , <i>Ananas comosus</i> , <i>Citrus sinensis</i>)	Wanapat et al. [65]	Peel	150 g/kg DM	−25.09	0.096

VFA: volatile fatty acids; ß: beta value; is considered significant with $p \leq 0.05$.

4. Discussion

Ruminant production significantly contributes to methane emissions; therefore, it is essential to analyze mitigation strategies in the dietary context of ruminal fermentation [67]. The rumen hosts a highly specialized ecosystem (bacteria, archaea, ciliated protozoa, anaerobic fungi, among others), and their interactions regulate the flow of carbon and electrons during fermentation [68]. The composition of the basal diet (DM, NDF, and ADF), starch, and ether extract determines the predominant fermentation pattern and hydrogen availability [69].

High-fiber diets favor fibrolytic bacteria, such as *Ruminococcus albus*, *Ruminococcus flavefaciens*, and *Fibrobacter succinogenes*, promoting the formation of acetate, CO₂, and H₂ [54], and consequently, increasing the supply of reducing equivalents for methanogenesis [70]. Conversely, diets with a higher starch content stimulate amylolytic and succinate/propionate-producing bacteria, such as *Prevotella* spp., *Selenomonas ruminantium*, and *Megasphaera elsdenii*, which compete for H₂ by promoting propionate formation [71,72]. In this sense, the effect of secondary metabolites supplemented by plant-based additives on the productive response of ruminants comprises a complex network of interactions between microbial ecology, fermentation dynamics, diet type, and host metabolism [73,74].

4.1. Effect of Secondary Metabolites on Methane Production

Ku-Vera et al. [9] observed that the use of plant-based secondary metabolites has emerged as a strategy to modulate fermentation processes and redirect hydrogen flow toward alternative pathways away from methane (CH₄) production.

4.1.1. Tannins

The present meta-analysis demonstrates that the application of plant-based additives rich in phenolic compounds, such as tannins, reduces methane production. This reduction indicates an improvement in the fermentative efficiency of the diet [72]. The effect of tannins on CH₄ production per unit of DM intake (g/kg) indicates that the observed modulation appears to involve a modification in the metabolic pathways responsible for its formation [75]. From a microbiological standpoint, methanogenesis in the rumen predominantly occurs via the hydrogenotrophic pathway, although methylotrophic and acetoclastic pathways also exist [6,76]. The hydrogenotrophic pathway (CO₂ + 4H₂ → CH₄) contributes to over 80% of the methane produced in the rumen and is principally mediated by archaea of the genus *Methanobrevibacter* [67].

The reduction in methane production following tannin administration indicates a direct impact on methanogenic activity or H₂ availability. Secondary metabolites intervene through various mechanisms, including indirect limitation of available H₂ via alterations in the fermentation pattern [9], direct inhibition of methanogenic archaea [77], modification of bacterial and archaeal membrane permeability [6], reduction in key enzyme activities such as methyl-coenzyme M reductase, which is responsible for the final step in methane synthesis [75] and a decrease in the interspecific transfer of H₂ to archaea associated with protozoal surfaces due to a defaunation effect that diminishes microbial populations [78]. This phenomenon impairs the efficiency of methanogenesis [79] and provides evidence that certain secondary metabolites may reduce the abundance of methanogenic archaea, such as *Methanosphaera*, while simultaneously increasing the relative abundance of cellulolytic bacteria, such as *Fibrobacter* [80], thereby confirming a restructuring of the microbial ecosystem rather than a mere direct inhibitory effect of the secondary metabolites.

Additionally, the considerable variability in the inclusion rates in this study, especially of tannins (mean = 17.32, CV = 170.4%), aligns with Orzuna-Orzuna et al. [17] who in a meta-analysis reported ranges between 0.46 and 60 g/kg DM, and Jayanegara et al. [78], who used 40, 59, and 79 g/kg DM, respectively. This demonstrates that the magnitude of the effect depends on the administered dose. Jayanegara et al. [78] reported a significant linear decrease in methane emissions as the concentration of tannins in the diet increased (0.109 mL CH₄ per additional g/kg DM of tannins supplied). Similarly, Orzuna-Orzuna et al. [17] confirmed that tannin supplementation effectively reduced enteric methane emissions in cattle; however, in addition to the inclusion dose, they highlighted the importance of the source and type of tannins as determinants of the observed response.

4.1.2. Flavonoids and Monoterpenes

The results of this review indicate that other classes of plant secondary metabolites, particularly flavonoids and monoterpenes, could produce even greater reductions in methane emissions relative to the feed intake. Although these results should be analyzed with caution due to the small number of comparisons and the lack of analysis of the risk of publication bias, the anti-methanogenic effect of flavonoids and monoterpenes may be associated with alterations in the relative abundance of archaea belonging to the genus *Methanobrevibacter* [75], which constitutes the predominant methanogenic group in the bovine rumen, particularly the species related to *M. gottschalkii* and *M. ruminantium* [68]. The modulation of these species has been linked to reductions in methane emissions

(mL/g DM) of 27.3% and 6.87%, respectively, when supplemented with 30 and 50 mg/L of *Pinus densiflora* extract, which is a rich source of bioactive compounds such as flavonoids and terpenes [81]. The results of this meta-analysis regarding the effects of flavonoids and monoterpenes on CH₄/DM intake (g/kg) suggest that these secondary plant metabolites not only decrease the relative abundance of methanogens but also modify the overall hydrogen balance within the fermentation system [72], and that methane mitigation may not depend only on the inclusion rate, but also on the specific phytochemical profile of the additive.

4.2. Effect of Secondary Metabolites on Fermentation Parameters

4.2.1. Tannins

The redistribution of hydrogen is also reflected in the volatile fatty acid profiles. The increase in propionate proportion observed with tannin supplementation supports the hypothesis that reducing equivalents are redirected toward gluconeogenic pathways, thereby diminishing the availability of electrons for methanogenesis [72,82]. Indeed, it has been reported in the literature that a higher relative abundance of *Prevotellaceae* and *Succinivibrionaceae* is negatively associated with methane emissions, as they compete for H₂ [83]. From an energetic standpoint, this redistribution indicates that some of the energy conserved by mitigating methane production could be redirected toward other fermentation pathways, thereby enhancing the efficiency of metabolizable energy utilization from the diet [72].

Furthermore, certain polyphenols can promote enzymes involved in the succinate pathway, which is associated with propionate synthesis [84]. This effect favors the proliferation of propionate-producing bacteria, such as *Prevotellaceae* and *Veillonellaceae*, and contributes to the enhanced stability of ruminal pH [85], which explains the alkalinization of the rumen environment with tannin supplementation through plant-based additives.

Although tannin supplementation showed no effects on acetate production and the A:P ratio, the latter has metabolic significance. Acetate production enhances the availability of reducing equivalents for methanogenesis, whereas propionate synthesis functions as an alternative hydrogen sink [70].

4.2.2. Terpenes and Terpenoids

Each group of metabolites may promote or inhibit different microbial populations responsible for the synthesis of acetate, propionate, or butyrate [86]. The effects observed with terpenes and terpenoids were homogeneous (I^2) and significant but without publication bias analysis, suggesting contrasting effects. Terpenes promoted the production of propionate and butyrate, whereas terpenoids showed a strong capacity to reduce ruminal fermentation but increased rumen pH. The results of this study suggest that the redistribution of hydrogen produced during ruminal fermentation is not uniform and can vary with the specific type of secondary metabolite present and its selective influence on microorganisms and predominant fermentation pathways. For example, terpenoids exhibit strong antimicrobial activity that can affect the proliferation of ruminal bacteria [87].

4.2.3. Phenolic Compounds

Overall, phenolic compounds increased the total VFA concentration (mmol/L) relative to the control. This suggests that the reduction in CH₄ did not lead to a decline in fermentative activity but rather a reorientation of ruminal metabolism, thereby illustrating that methane mitigation can be achieved without impairing total fermentative energy production [72].

Furthermore, the protozoa ($\times 10^5$ /mL) reduction observed after the administration of tannins, a type of phenolic compound, aligns with the previously documented reduction in

methanogenesis attributable to the defaunation effect of secondary metabolites on these protozoa and their symbiotic relationship with methanogenic archaea [78]. The biological efficacy of secondary metabolites depends on their dosage and effects on intake and digestibility [88].

4.3. Effect of Secondary Metabolites on Animal Performance and Nutrient Intake

From a bioenergy perspective, methane constitutes a loss of the gross energy consumed [72]. A reduction in methane production may increase the proportion of metabolizable energy retained, thereby fostering more efficient utilization for productive functions and potentially compensating for variations in digestibility [70]. However, despite modifications in fermentation processes and methane mitigation efforts, no adverse effects were observed with plant-based secondary metabolites on daily weight gain, final body weight, or feed efficiency. This finding aligns with those of Akanmu et al. [89], who assessed plant-based secondary metabolites from *Moringa oleifera*, *Jatropha curcas*, and *Aloe vera* (50 mg/kg DM feed) and concluded that methane mitigation can be achieved without detrimental effects on production parameters.

4.3.1. Tannins

The trend to enhance organic matter intake with tannins can be explained by the lower available dietary nitrogen in the rumen and the animals' ability to modulate their intake to meet their amino acid requirements [83]. It has been documented that high tannin concentrations (>5%) can form complexes with proteins [90,91] through hydrogen bonding and hydrophobic interactions. Consequently, these tannin–protein complexes reduce protein degradation within the rumen, leading to less microbial protein synthesis [86,92]. Consequently, a higher and lower proportion of rumen-undegraded and microbial protein, respectively, is delivered to the small intestine. Microbial protein provides at least half of the amino acids absorbed by ruminants [93]. The proliferation of rumen microorganisms depends on the availability of fermentable energy and degradable proteins in the rumen [94]. Reduced protein availability due to tannins affects bacterial proliferation [95] and the rumen's fermentative capacity, which could be limiting feed intake and, therefore, gross energy intake.

4.3.2. Flavonoids

This analysis demonstrated that the inclusion of flavonoids through plant-based additives was associated with a reduction in dry matter intake, with an average dosage of 7.19 g/kg DM and a maximum inclusion level of 50 g/kg DM. This phenomenon can be ascribed to the fact that certain flavanones diminish palatability by activating bitter taste receptors [96,97] and may exert astringent effects, potentially altering the feeding behavior [90]. This impact on dry matter intake contrasts with the findings of Balcells et al. [98] and Jiménez-Ocampo et al. [41], who incorporated flavanones at 0.06 g/kg DM and 1.5–3 g/kg DM, respectively, without reporting significant variations in this parameter, likely due to their lower inclusion levels compared to those reported in this meta-analysis.

4.4. Sources of Heterogeneity in the Response of Plant-Based Secondary Metabolites

Finally, secondary metabolites are widely distributed across various plant structures, with their specific localization depending on their chemical classification. For example, phenolic compounds primarily contribute to the coloration of flowers, fruits, and other pigmented tissues, whereas flavonoids are predominantly found in leaves, flowers, stems, and roots [99]. In addition, certain terpenoids are concentrated in the leaves of some species [100]. Correspondingly, the meta-regression analysis demonstrated that both the plant species and the botanical fraction employed for dietary supplementation or the extrac-

tion of secondary metabolites significantly influenced the extent of the anti-methanogenic effect, suggesting that the response is not solely determined by the type of secondary metabolite but also by its concentration, bioavailability, and specific phytochemical profile [101].

The plants listed in Table 6 are primarily characterized by their abundance of terpenoids, flavonoids, and tannins. Six of these plants are tree legumes belonging to the *Fabaceae* family [102], commonly recognized as the legume family, which holds significant economic value owing to its fruits, flowers, and leaves and is regarded as the third-largest terrestrial plant family [103]. Additionally, they include species from the *Anacardiaceae* family [104], which comprises approximately 82 genera and around 800 species [105], primarily trees and woody shrubs [106].

This family comprises several economically significant species, such as cashew, which are characterized by the presence of phenolic compounds [105]. The remaining species belong to other families, including *Fagaceae* [107], *Musaceae* [108], and *Euphorbiaceae* [109]. An in vitro study using ruminal inoculum from dairy cows and a species from the *Fagaceae* family indicated that adding this species reduced methane production by up to 40% relative to the control as its concentration increased (≥ 50 g kg/d) [110]. Additionally, another study by Dagaew et al. [111] using 3% banana flower (*Musaceae* family) in an artificial simulation of the bovine rumen observed a 14.5% decrease in methane production ($p \leq 0.05$) compared to the control, which was attributed to a reduction in methanobacteria.

The secondary metabolites found in these herbs directly affect ruminal fermentation, thereby reinforcing the notion that the effect depends on the specific phytochemical profile of each herb. For instance, the application of banana flowers has been shown to influence ruminal microbial communities, resulting in a significant reduction in methane (CH_4) levels (mmol/L), which is attributed to their phenolic compound content. Reported reductions of 10.7% and 18.9% were observed at inclusion rates of 30 and 60 g/kg dry matter (DM), respectively, compared with the control.

Similarly, extracts of chestnut wood (40 g/day) and *Acacia* spp. (1.25% and 2.5%, characterized by their high tannin content) significantly reduced daily methane production by up to 21.6% [48] and 33% [38], respectively, compared with that in the control. All of this information suggests that the magnitude of the effect observed across studies may be associated with variability in the phytochemical profile of the plant resources evaluated, their chemical structure, their bioavailability within the plant matrix, and the selective interaction they exert on different microbial groups in the rumen (methanogens, protozoa, and H_2 -competing bacteria). These interactions may alter fermentation patterns and account for some of the heterogeneity observed in the ruminal microbiota's antimethanogenic response to the addition of plant-based secondary metabolites, which varies depending on the plant species, dose, and experimental conditions.

Taken together, these results highlight the importance of concurrently evaluating the basal diet, specific metabolite type, administered dose, and plant fraction used to develop nutritional strategies to reduce methane emissions in beef cattle.

4.5. The Publication Bias

Publication bias refers to the preferential publication of statistically significant positive results, in which studies without significant or negative results are less likely to be published [112]. The publication bias observed in the response variables of this review indicates a lack of accurate representation of the current knowledge on the topic under study [113]. Although adjusting for publication bias in this study reduced the number of variables showing a significant effect of secondary metabolites, the methodological adjustment strengthened the study's results and scope by identifying that the available

results systematically differed from the missing results [114]. This avoids underestimation or overestimation of the observed treatment effects and reduces the risk of bias in decision-making due to benefit-risk imbalance [115]. Another challenge observed in our results was the limited number of cross-study comparisons for certain variables. Herbison et al. [116] state that one should be cautious when drawing definitive conclusions from results generated with a few comparisons. However, they also mentioned that a few trials are sufficient to obtain a reasonably robust answer.

5. Conclusions

This meta-analysis demonstrated that supplementation with plant-based additives rich in tannins significantly reduced enteric methane production in beef cattle, especially when emissions were expressed relative to dry matter intake (g/kg DM). The findings presented here underscore the potential of tannins as a viable nutritional strategy to enhance fermentation efficiency, sustain animal productivity, and mitigate the environmental impact of beef cattle production. However, in this study, factors such as the type of compound, dosage, composition of the basal diet, small number of comparisons, and publication bias should be considered when evaluating the effects observed with tannins, flavonoids, terpenes, terpenoids, and phenolic compounds.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/ruminants6030053/s1>. Table S1: Search formulas for databases, filters applied, and number of articles found; Figure S1: Funnel plots for publication bias for methane production (a), animal performance (b), and ruminal fermentation profile (c); Figure S2: Trim-and-fill funnel plots for methane production (a), animal performance (b), and ruminal fermentation profile (c).

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