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Full adoption of the most effective strategies to mitigate methane emissions by ruminants can help meet the 1.5 °C target by 2030 but not 2050

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To meet the 1.5 °C target, methane (CH_4) from ruminants must be reduced by 11 to 30% by 2030 and 24 to 47% by 2050 compared to 2010 levels. A meta-analysis identified strategies to decrease product-based (PB; CH_4 per unit meat or milk) and absolute (ABS) enteric CH_4 emissions while maintaining or increasing animal productivity (AP; weight gain or milk yield). Next, the potential of different adoption rates of one PB or one ABS strategy to contribute to the 1.5 °C target was estimated. The database included findings from 430 peer-reviewed studies, which reported 98 mitigation strategies that can be classified into three categories: animal and feed management, diet formulation, and rumen manipulation. A random-effects meta-analysis weighted by inverse variance was carried out. Three PB strategies—namely, increasing feeding level, decreasing grass maturity, and decreasing dietary forage-to-concentrate ratio—decreased CH_4 per unit meat or milk by on average 12% and increased AP by a median of 17%. Five ABS strategies—namely CH_4 inhibitors, tanniferous forages, electron sinks, oils and fats, and oilseeds—decreased daily methane by on average 21%. Globally, only 100% adoption of the most effective PB and ABS strategies can meet the 1.5 °C target by 2030 but not 2050, because mitigation effects are offset by projected increases in CH_4 due to increasing milk and meat demand. Notably, by 2030 and 2050, low- and middle-income countries may not meet their contribution to the 1.5 °C target for this same reason, whereas high-income countries could meet their contributions due to only a minor projected increase in enteric CH_4 emissions.

methane | meta-analysis | ruminant | enteric | mitigation

Global food systems contribute up to 30% of the worldwide greenhouse gas (GHG) emissions (1). The goal of the Paris Agreement, to limit global warming to 1.5 °C above preindustrial levels, is unlikely to be achieved if food systems continue operating on a business-as-usual (BAU) scenario (1). Among food-related GHG emissions, methane (CH_4) from livestock contributes 30% of the global anthropogenic CH_4 emissions (2), 17% of the global food system GHG emissions, and 5% of global GHG emissions (2, 3). Of the global livestock CH_4 emissions, 88% is contributed by enteric fermentation (4).

Methane is a short-lived climate pollutant. Given its perturbation lifetime in the atmosphere of around 12.5 y, CH_4 contributes significantly to near-term global warming (5). Its global warming potential is 84 or 28 for 20- or 100-y time horizons, respectively (5). When evaluating the contribution of global food systems to CH_4 emissions over a 20-y period instead of the commonly used 100-y time period for national GHG inventories, the contribution of CH_4 to food system GHG emissions more than doubles, from 17 to 36% (3, 5).

The realization of nationally determined contributions and 2050 climate neutrality goals depends upon the reduction of CH_4 emissions. Within sectoral reductions of CH_4 emissions, technical solutions to decrease CH_4 from agricultural production—especially strategies to mitigate CH_4 from enteric fermentation by ruminant livestock—are integral to meeting these climate targets, but quantitative data on mitigation potentials are scarce (6). Based on 2010 GHG emission levels and different mitigation scenarios to limit global warming to 1.5 °C, agricultural CH_4 emissions need to be decreased by 11 to 30% by 2030 and by 24 to 47% by 2050 (7).

The global population is projected to increase by 23% between 2010 and 2030, with most of the increase occurring in low- and middle-income countries (LMIC) (8). Ruminants contribute about half of the animal protein produced by livestock (4). In

Significance

Agricultural methane emissions must be decreased by 11 to 30% of the 2010 level by 2030 and by 24 to 47% by 2050 to meet the 1.5 °C target. We identified three strategies to decrease product-based methane emissions while increasing animal productivity and five strategies to decrease absolute methane emissions without reducing animal productivity. Globally, 100% adoption of the most effective product-based and absolute methane emission mitigation strategy can meet the 1.5 °C target by 2030 but not 2050, because mitigation effects are offset by projected increases in methane. On a regional level, Europe but not Africa may be able to meet their contribution to the 1.5 °C target, highlighting the different challenges faced by high- and middle- and low-income countries.

The authors declare no competing interest.

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LMIC, ruminant livestock play a crucial role in food security (9). Ruminants can convert human-inedible feeds, like those from pastures and grain commodity by-products produced on marginal lands or from subsistence agricultural production systems, into nutritionally dense human-edible foods. Ruminants also provide other benefits, such as traction and manure for fuel and fertilizer (10). In addition, human population growth is generally high in LMIC, while consumption of animal-sourced food is often below recommended dietary levels or reliant upon ruminant meat and milk for livelihoods and nutrition security (10, 11). Thus, from a feed-food competition perspective, ruminant production increases in LMIC should rely on human inedible feeds (i.e., forage and by-products). In contrast, in high-income countries (HIC) population growth is much lower and the consumption of animal protein is often above recommended dietary levels (9, 11).

Sustainable strategies for enteric CH_4 mitigation that align with the 1.5 °C target should preferably avoid socioeconomic and environmental tradeoffs (12) and, ideally, increase production yield per unit of input. Reductions in both CH_4 emissions intensity (i.e., emissions per unit of milk and gain [CH_4I_M and CH_4I_G, respectively]) and absolute CH_4 emissions are therefore needed. Strategies that reduce CH_4I and increase production per unit of input could be used to expand food production from the existing ruminant population without increasing total CH_4 emissions (13–15), and thus contribute to the 1.5 °C target as well as to sustainable development goals. Several reviews indicate that animal and feed management, diet formulation, and rumen manipulation strategies could significantly decrease enteric CH_4 emissions (12, 16, 17). However, previous studies consisted of qualitative reviews (12), examined the quantitative effects of a single mitigation strategy (18–20), or compared CH_4 yield (CH_4Y; CH_4 per unit of feed intake) between multiple mitigation strategies (17). Methane yield is only one relevant measure, and other major CH_4 emission and animal performance metrics must be considered to determine the effectiveness and feasibility of mitigation strategies. Only one recent publication examined the quantitative effects of multiple mitigation strategies on CH_4 emission and animal performance metrics, but the analysis was limited to Latin America (21). Important CH_4 emission metrics include daily CH_4 emissions, CH_4Y, or CH_4-energy conversion factor [Y_m; CH_4 energy as a proportion of gross energy intake; a component of the tier 2 calculation for national GHG inventories recommended by the Intergovernmental Panel on Climate Change (22)], CH_4I_G, and CH_4I_M. Important animal performance metrics include feed intake, nutrient digestibility, and animal productivity (AP).

The objective of this study was to conduct a comprehensive meta-analysis of enteric CH_4 mitigation strategies published in peer-reviewed journals by examining their quantitative effect on the aforementioned in vivo CH_4 emissions and animal performance metrics and to estimate their potential to contribute to the 1.5 °C target. As outlined above, there is an urgent need for strategies that can effectively mitigate enteric CH_4 emissions without negatively affecting AP by focusing exclusively on strategies that decouple CH_4 emissions from animal production (23). Mitigation effects were quantified on a global level as well as on a regional level. The African and European regions were selected to represent LMIC and HIC, respectively.

Results and Discussion

The meta-analysis included 98 mitigation strategies reported in 430 peer-reviewed journal publications (*SI Appendix*, Table S1). Mitigation strategies were classified into three main categories: animal and feed management, diet formulation, or rumen manipulation strategies. Of the strategies included, 63 did not significantly (adjusted $P \geq 0.05$) decrease daily CH_4 emissions; the remaining 35 strategies decreased daily CH_4 emissions by on average 18% (ranging from 5 to 43%). These strategies were classified as "effective" in decreasing product-based CH_4 (PB strategies) if they significantly decreased CH_4I_M or CH_4I_G and CH_4Y while significantly (adjusted $P < 0.05$) increasing AP. Strategies were classified as effective in decreasing absolute CH_4 emissions (ABS strategies) if they significantly decreased daily CH_4 emissions, CH_4I_M or CH_4I_G, and CH_4Y without decreasing AP (weight gain of growing animals or milk yield of lactating dairy animals) when productivity data were present.

A summary of the studied mitigation strategies is presented in Fig. 1, and the full list of the studied mitigation strategies and their effects on enteric CH_4 emission and animal performance metrics are presented in *SI Appendix*, Table S2 and Dataset S1, respectively. Effective mitigation strategies and their impact on CH_4I_M, CH_4I_G, daily CH_4, CH_4Y, as well as their relevance for different systems (feedlot, mixed, and grassland) are presented in Fig. 2 from highest to lowest efficacy in reducing CH_4I_M. All other strategies that were not classified as effective but had a significant effect on CH_4, CH_4Y, Y_m, CH_4I_G, or CH_4I_M are presented in *SI Appendix*, Figs. S1–S3.

The meta-analysis identified three effective PB strategies, namely: increasing feeding level, decreasing grass maturity, and decreasing dietary forage-to-concentrate ratio. These PB strategies decreased CH_4I by on average 12% (range 9 to 17%) and increased AP by a median of 17% (range 9 to 162%). Furthermore, there were five effective ABS strategies, namely: CH_4 inhibitors, tanniferous forages, electron sinks, oils and fats, and oilseeds (only for lactating animals, since oilseed supplementation significantly decreased weight gain in growing animals). These ABS strategies decreased CH_4I by on average 17% (ranging from 12 to 32%) and daily CH_4 emissions by on average 21% (ranging from 12 to 35%) without negatively affecting AP.

Several mitigation strategies were excluded from the present evaluation or classified as ineffective because of insufficient publications. These include breeding low-CH_4–emitting animals and improving animal health. However, modeling studies have shown that strategies that improve animal health may significantly increase AP and reduce CH_4I (24). In the subsequent section, the effects of mitigation strategies are reported in parenthesis as mean, 95% CI, and the number of treatment comparisons (*n*). Reported differences were significant (adjusted $P < 0.05$) unless indicated otherwise.

Strategies that Decrease PB CH_4 Emissions and Increase Production. Increasing feeding level (mean = 58%, 95% CI = 47 to 71%, $n = 47$) decreased CH_4I_M (17%, 9 to 23%, $n = 5$). No data were available for CH_4I_G. Fiber digestibility was decreased (7%, 2 to 12%, $n = 18$), likely due to increased rumen passage rates (25). Increasing feed intake resulted in increased weight gain (162%, 38 to 398%, $n = 7$) and milk yield (17%, 10 to 25%, $n = 8$). Increasing feed intake to improve AP significantly decreases CH_4I_G and CH_4I_M (12, 26) as well as the overall carbon footprint of animal-sourced food (27) when diet composition remains unchanged. This strategy directs energy for CH_4 toward animal production (28) but also decreases energy requirements for maintenance relative to milk production and reduces the time to slaughter for growing animals. Potential effects of this practice on manure CH_4 emissions, as a result of decreased fiber

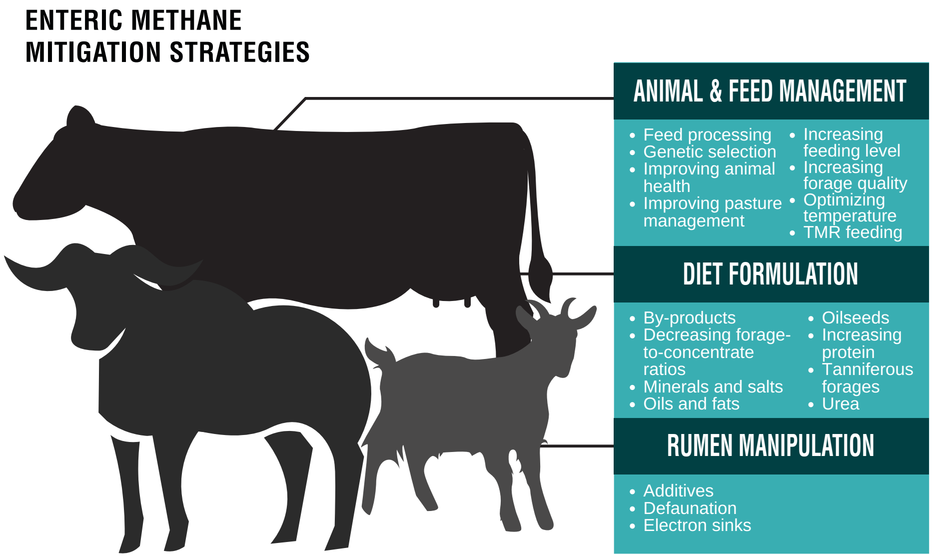


Fig. 1. Studied enteric methane mitigation strategies. For a complete list of strategies, see *SI Appendix*, Table S2.

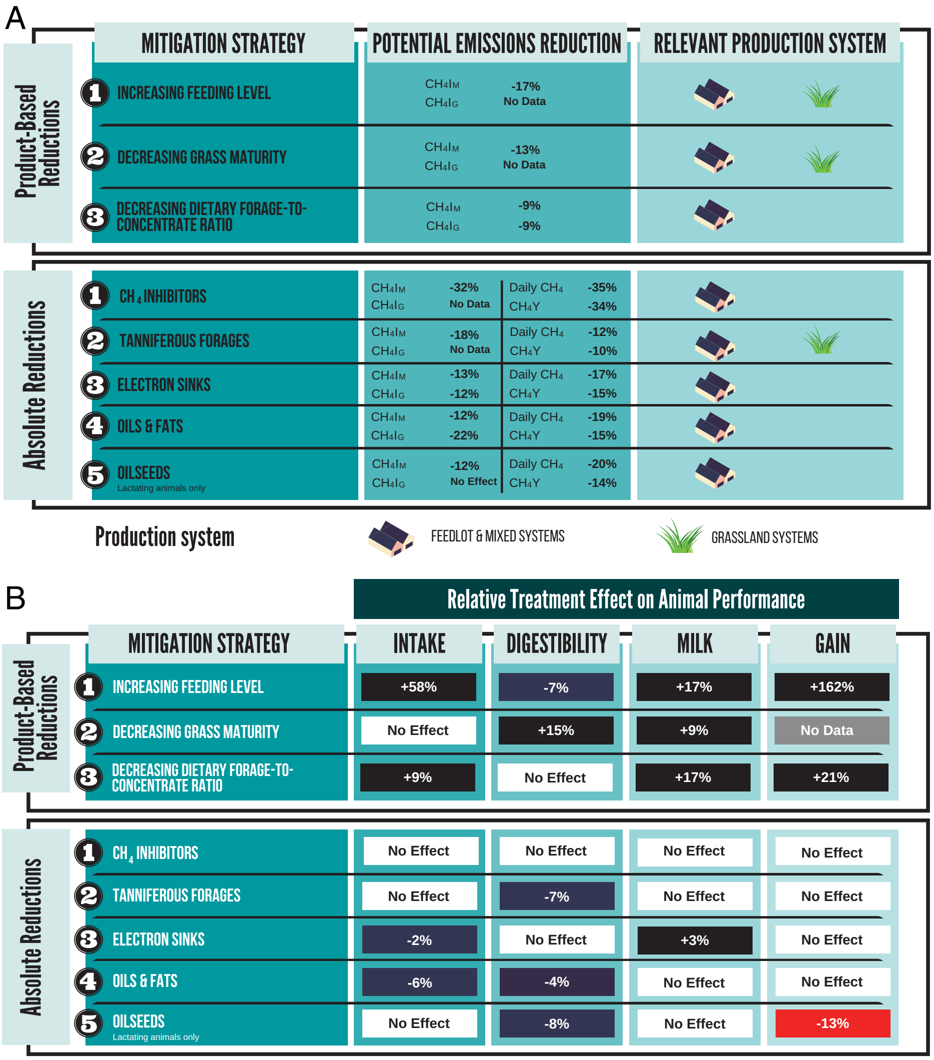
digestibility, need to be evaluated. The practice is applicable to feedlots, mixed, and grassland systems, but particularly the latter and especially in certain climatic regions where animals are underfed due to insufficient or low quality forage (29).

Decreasing grass maturity decreased CH_4I_M (13%, 7 to 18%, $n = 6$), did not affect feed intake, but increased milk yield (9%, 1 to 18%, $n = 6$). Furthermore, it improved fiber digestibility (15%, 9 to 21%, $n = 9$), which can potentially decrease manure CH_4 emissions (22). The positive effect of decreasing grass maturity on milk yield is likely attributed to greater digestible energy and protein content. Increased protein content, however, can lead to increased nitrogen intake and excretion (30). Thus, possible tradeoffs associated with direct and indirect manure nitrous oxide emissions require further evaluation. Decreasing grass maturity is applicable to all production systems. Although this strategy increases the overall efficiency of dietary nutrient use for milk production (kg milk unit of feed intake^{-1}), it was not deemed to be cost-effective in The Netherlands; however, it was more cost-effective than supplementation with nitrate or linseed (31).

Decreasing dietary forage-to-concentrate ratio decreased CH_4I_M (9%, 4 to 14%, $n = 19$) and CH_4I_G (9%, 3 to 15%, $n = 16$). It increased feed intake (9%, 5 to 14%, $n = 85$), which led to an increase in weight gain (21%, 13 to 29%, $n = 32$) and milk yield (17%, 10 to 24%, $n = 26$) but did not increase absolute CH_4 emissions or reduce fiber digestibility. Reduced CH_4Y (13%, 10 to 16%, $n = 69$) was the result of increased feed intake, which most likely resulted in a shift in rumen fermentation patterns and a decrease in rumen pH, which inhibits methanogens (32). However, the supplementation of grain-based concentrate needs to be limited because overfeeding can lead to subacute ruminal acidosis. Subacute ruminal acidosis is a nutritional disease that is mostly found in the feedlot and high-yielding dairy cattle. It is associated with perturbation of rumen fermentation, decreased fiber digestibility, milk fat content, and animal health (33). In addition, the promotion of increased use of (food-quality) grain-based concentrate in ruminant diets will likely intensify feed-food competition. In contrast, if concentrate-rich diets are mainly based on food industry by-products, the feed-food competition may be avoided. The cost-effectiveness of this strategy will depend on forage and concentrate costs as well as associated increases in animal production and the price of animal products (meat and milk).

Strategies that Decrease Absolute CH_4 Emissions. Rumen manipulation by feeding CH_4 inhibitors effectively decreased CH_4I_M (32%, 21 to 40%, $n = 2$) without affecting feed intake or milk yield. Of the CH_4 inhibitors, 3-nitrooxypropanol (3-NOP) acts on a key enzyme of the methanogenesis pathway that is used by methanogenesis to produce CH_4 (34). Insufficient data were available in the database to evaluate its effect on weight gain or fiber digestibility in this analysis. However, in recent studies, 3-NOP did not show adverse effects on weight gain of growing beef cattle (35) or fiber digestibility in early-lactation dairy cows (36) and decreased daily CH_4 emissions throughout a 15-wk experiment (37). A recent meta-analysis showed that 3-NOP decreased daily CH_4 emissions in a dose-dependent manner, that its mitigation effect was greater for dairy than beef cattle, and that its effectiveness decreased with increasing dietary fiber content (18). In its current form, 3-NOP can only be used in confinement systems because it is more effective when fed continuously (36, 38), but ongoing research is developing mechanisms for its application under grazing conditions (39). Supplementation of 3-NOP increased milk fat content in dairy cattle (29) and feed efficiency in feedlot cattle (40), which may help offset its cost and stimulate adoption. A limitation of 3-NOP is that its use as a feed additive requires regulatory approval by various countries. Another CH_4 inhibitor strategy is supplementation with seaweed (e.g., *Asparagopsis taxiformis*), which can decrease daily CH_4 emissions by up to 80% (41). However, more research is warranted on dietary inclusion levels, effects on animal feed intake and production (42), the implications and safety of feeding bromoform (43), its main active compound (44), the extremely high iodine content of *Asparagopsis* species (which limits how much can be fed in many countries), as well as the environmental effects of cultivating seaweed (45) before it can be recommended as a mitigation strategy.

Dietary inclusion of tanniferous forages decreased CH_4I_M (18%, 8 to 26%, $n = 7$). However, it also decreased fiber digestibility (7%, 2 to 12%, $n = 21$), which could potentially increase manure CH_4 emissions (22). Daily CH_4 emissions were also decreased (12%, 7 to 16%, $n = 42$) and feed intake



A

	MITIGATION STRATEGY	POTENTIAL EMISSIONS REDUCTION		RELEVANT PRODUCTION SYSTEM
Product-Based Reductions	① INCREASING FEEDING LEVEL	CH_4I_M -17% CH_4I_G No Data		🏠 🌿
	② DECREASING GRASS MATURITY	CH_4I_M -13% CH_4I_G No Data		🏠 🌿
	③ DECREASING DIETARY FORAGE-TO-CONCENTRATE RATIO	CH_4I_M -9% CH_4I_G -9%		🏠
Absolute Reductions	① CH_4 INHIBITORS	CH_4I_M -32% CH_4I_G No Data	Daily CH_4 -35% CH_4Y -34%	🏠
	② TANNIFEROUS FORAGES	CH_4I_M -18% CH_4I_G No Data	Daily CH_4 -12% CH_4Y -10%	🏠 🌿
	③ ELECTRON SINKS	CH_4I_M -13% CH_4I_G -12%	Daily CH_4 -17% CH_4Y -15%	🏠
	④ OILS & FATS	CH_4I_M -12% CH_4I_G -22%	Daily CH_4 -19% CH_4Y -15%	🏠
	⑤ OILSEEDS Lactating animals only	CH_4I_M -12% CH_4I_G No Effect	Daily CH_4 -20% CH_4Y -14%	🏠

Production system 🏠 FEEDLOT & MIXED SYSTEMS 🌿 GRASSLAND SYSTEMS

B

		Relative Treatment Effect on Animal Performance			
	MITIGATION STRATEGY	INTAKE	DIGESTIBILITY	MILK	GAIN
Product-Based Reductions	① INCREASING FEEDING LEVEL	+58%	-7%	+17%	+162%
	② DECREASING GRASS MATURITY	No Effect	+15%	+9%	No Data
	③ DECREASING DIETARY FORAGE-TO-CONCENTRATE RATIO	+9%	No Effect	+17%	+21%
Absolute Reductions	① CH_4 INHIBITORS	No Effect	No Effect	No Effect	No Effect
	② TANNIFEROUS FORAGES	No Effect	-7%	No Effect	No Effect
	③ ELECTRON SINKS	-2%	No Effect	+3%	No Effect
	④ OILS & FATS	-6%	-4%	No Effect	No Effect
	⑤ OILSEEDS Lactating animals only	No Effect	-8%	No Effect	-13%

Fig. 2. Effective mitigation strategies and their effect on methane (CH_4) emissions (*A*) and animal performance metrics (*B*). CH_4I_M = CH_4 emission intensity for milk (g CH_4 kg of milk^{-1}); CH_4I_G = CH_4 emission intensity for weight gain (g CH_4 kg of weight gain for growing animals^{-1}); daily CH_4 = daily CH_4 emissions (g animal^{-1} d^{-1}); digestibility = apparent digestibility of neutral detergent fiber (%); gain = average daily gain (kg d^{-1}); intake = dry matter intake (kg d^{-1}); milk = milk yield (kg d^{-1}); when numeric values are shown a significant effect was observed (adjusted $P < 0.05$) and no effect when adjusted $P \geq 0.05$.

or animal production were unaffected. There are differences in efficacy among tannin sources. *Sericea lespedeza* (*Lespedeza cuneata*) and *Lotus* (*Lotus corniculatus* and *Lotus pedunculatus*) were determined as the most promising tanniferous forage as they significantly decreased daily CH_4 emissions (32% and 8%, respectively) without affecting feed intake. *S. lespedeza* (*L. cuneata*) decreased daily CH_4 emissions (32%, 24 to 39%, n = 5) without affecting feed intake in goats and it has been effective in decreasing daily CH_4 emissions throughout a 12-wk experiment (46). Other tanniferous forages that may potentially decrease daily CH_4 emissions are *Leucaena* (8%, 0 to 16%, n = 12, P = 0.10) and *Lotus* (*L. corniculatus* and *L. pedunculatus*) (8%, 3 to 13%, n = 3). Although this meta-analysis did not reveal any effect on feed intake, tanniferous forages have been associated with decreased palatability and feed intake (47). In addition, tannins can bind to dietary protein and thus decrease protein digestion and animal production, especially when dietary protein is limiting. Nevertheless, when dietary protein is excessive or highly degradable, tannins may be beneficial because they reduce the excretion of nitrogen in urine, which decreases ammonia and nitrous oxide emissions from manure (48). The cost-effectiveness of their supplementation still needs to be evaluated. Among the identified effective ABS strategies, dietary inclusion of tanniferous forages is the only one applicable to grassland besides feedlot and mixed systems. As 37% of global enteric CH_4 emissions from ruminant livestock is attributed to grazing systems (4), it will be important to identify other effective ABS strategies that are applicable to grassland systems.

Rumen manipulation with electron sinks decreased CH_4I_M (13%, 9 to 16%, n = 12) and CH_4I_G (12%, 2 to 20%, n = 3). Although they led to small decreases in feed intake (2%, 1 to 3%, n = 49), small increases in milk yield (3%, 1 to 5%, n = 13) were observed. Electron sinks accept hydrogen that would otherwise be used by methanogens for CH_4 production in the rumen (32). Of the studied electron sinks (fumaric acid and nitrate), only nitrate was classified as effective. Nitrate has been shown to decrease daily CH_4 emissions and CH_4Y in a dose-dependent manner with no loss of effectiveness and effectively decreased daily CH_4 emissions over the long term (20, 49). Similar to 3-NOP, nitrate was more effective in decreasing daily CH_4 emissions and CH_4Y in dairy than in beef cattle (20). Although nitrate can be toxic, early research on nitrate supplementation in ruminant diets reported a decrease in feed intake and no toxicity symptoms; however, toxicity can occur if animals are not properly acclimatized (50). Acclimatization of animals to dietary nitrate is required to avoid methemoglobinemia, a blood disorder in which too little oxygen is delivered to the cells. However, this acclimatization can be lost within 3 wk when nitrate is not fed daily (51). Simultaneous sulfate supplementation has been shown to help protect cattle against nitrate toxicity (52). Nitrate supplementation may increase enteric and possibly manure nitrous oxide emissions (53). Studies in France (54) and The Netherlands (31) found that nitrate supplementation was not cost-effective.

Dietary inclusion of oil and fat decreased CH_4I_M (12%, 6 to 18%, $n = 24$) and CH_4I_G (22%, 8 to 35%, $n = 6$); however, possible effects on manure CH_4 emissions due to decreased fiber digestibility (4%, 2 to 7%, $n = 37$) need to be evaluated (22). Weight gain in growing animals or milk production in dairy animals was unaffected despite decreasing feed intake (6%, 3 to 8%, $n = 58$) and fiber digestibility, likely because of the high energy concentration of lipids compared with the feeds it replaces in livestock diets. Of the subcategories included in oil and fat supplementation, only dietary inclusion of predominantly vegetable oils effectively decreased daily CH_4 emissions. This effect can be attributed to increased supply of nonfermentable highly digestible energy, decreased feed intake and fiber digestibility, as well as inhibition of methanogenesis by unsaturated (or medium-chain saturated) fatty acids, which are usually abundant in vegetable oils. Oil inclusion reportedly decreases daily CH_4 emissions in a dose–response manner (19) and over the long term (55, 56). The amount of oil that can be included in ruminant diets, however, is limited and inclusion level should not be at the expense of healthy rumen fermentation to avoid negative impact on animal health and productivity (57). Maximum oil inclusion levels in ruminant diets depend on the animal's physiological stage, lipid and other nutrient composition of the basal diet, and fatty acid profile of the supplemental oil (58). Dietary oils and fats are by-products of oilseed production. Oilseed production has been associated with a near doubling of upstream GHG emissions per kg dry matter compared with other concentrate feeds (1.27 vs. 0.70 CO_2 equivalents kg dry matter^{-1}) (59). Thus, upstream emissions are likely to increase when concentrate feeds are substituted by oil and fat. However, enteric fermentation usually contributes substantially more GHG to the carbon footprint of ruminant products than feed production (60, 61) and the dietary inclusion of oil is limited. Thus, increases in upstream emissions are unlikely to offset GHG reduction through the mitigation of enteric CH_4 emissions by oils or fats. Nevertheless, exact upstream offsets of oils should be evaluated. The cost-effectiveness of feeding oils to decrease CH_4I varies by region and country, because the price of oil, as well as meat and milk, vary considerably therein. Studies in China (62), France (54), and The Netherlands (31) found that dietary inclusion of oils, for the purpose of mitigating enteric CH_4 emissions, was not cost-effective, but trade-offs by concomitant improvements in the fatty acid profile of milk and meat from a human health perspective might help to support the adoption of certain oils and oilseeds in animal diets.

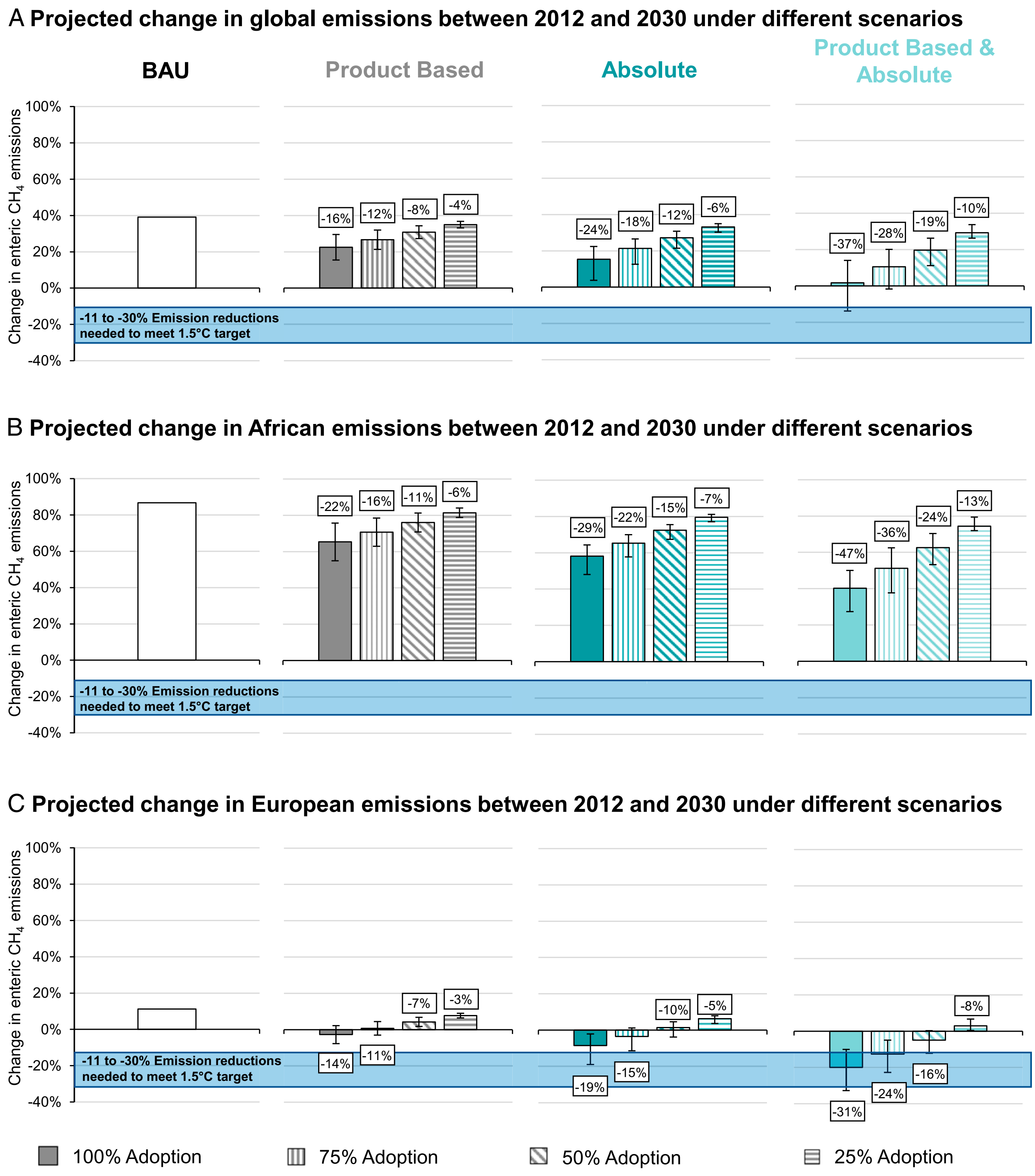
Dietary inclusion of oilseeds (cracked or crushed) had similar effects on CH_4I_M (12%, 4 to 19%, $n = 6$) compared with oils and fat. Their supplementation tended to decrease feed intake (4%, 1 to 7%, $n = 25$, $P = 0.06$) and decreased fiber digestibility (8%, 6 to 11%, $n = 13$). Similar to oils, oilseeds had no effect on milk yield but decreased weight gain in growing animals (13%, 6 to 20%, $n = 8$); thus, dietary oilseed inclusion may only be recommended for lactating animals and not for growing animals. Likewise, the amount of inclusion of oilseeds should be limited to avoid negative impacts on rumen fermentation, animal health, and production. However, as part of the oil in oilseeds is rumen-protected, dietary oil inclusion levels can be slightly higher than that of pure oils (63). And similar to oil inclusion, the possible impact to manure CH_4 emissions due to decreased fiber digestibility needs to be evaluated. Oilseeds that tended to decrease CH_4I_M were cottonseed (15%, 2 to 25%, $n = 2$, $P = 0.07$) and canola seed (13%, 2 to 23%, $n = 3$, $P = 0.07$).

The Potential of the Identified Strategies to Decrease Enteric Methane Emissions. The potential of the identified strategies to decrease enteric CH_4 emissions globally, in Africa, and in Europe between 2012 and 2030 and between 2012 and 2050, was estimated using three mitigation scenarios. The year 2012 was used as the baseline instead of 2010, because projections used for demand (64) and human population (65) only had figures for 2012 and not 2010. The identified strategies in the current meta-analysis (Fig. 2) and BAU projections for per capita red meat and dairy food protein demand (64), together with Food and Agriculture Organization of the United Nations (FAO) projections for human population growth (65), were used in the mitigation scenarios. Although international trade allows livestock products to move across regions, it was assumed that demand increases in each of the modeled regions would be met by livestock production within the same region, an assumption that suggests technological, market, and policy conditions would allow each region to produce enough to meet their own livestock protein demand. A sensitivity analysis for 100%, 75%, 50%, and 25% adoption rates of mitigation measures was performed. The three mitigation scenarios were: 1) adoption of one PB strategy, 2) adoption of one ABS strategy, and 3) simultaneous adoption of one PB and one ABS.

Globally, only the 100% adoption of the most effective PB and ABS strategies (increasing feeding level and inclusion of a CH_4 inhibitor, respectively) decreased enteric CH_4 emissions sufficiently (14%) to meet the 1.5 °C target by 2030 (Fig. 3*A*) but not by 2050 (*SI Appendix*, Fig. S4*A*). In Africa, which was chosen to represent LMIC, none of the mitigation scenarios had the potential to meet the 1.5 °C target by 2030 or 2050 (Fig. 3*B* and *SI Appendix*, Fig. S4*B*). Although the 100% adoption of the most effective PB and ABS strategies was estimated to mitigate enteric CH_4 emissions by 47% and 76% between 2012 and 2030 and 2012 and 2050, respectively, the mitigation effect was offset by estimated increases in CH_4 emissions in the BAU scenario (87% and 220%, respectively) (Fig. 3*B* and *SI Appendix*, Fig. S4*B*).

In contrast, in Europe, which was chosen to represent HIC, projected increases in enteric CH_4 emissions between 2012 and 2030 and 2012 and 2050 without mitigation strategy (BAU scenario) were only 11% (Fig. 3*C* and *SI Appendix*, Fig. S4*C*). By 2030, Europe could meet the 1.5 °C target under the following mitigation scenarios (Fig. 3*C*): 1) the simultaneous 100% and 75% adoption of one PB strategy (when assuming the average or above average mitigation potential of all PB strategies) and one ABS strategy (when assuming the average or above average mitigation potential of all ABS strategies); 2) the simultaneous at least 50% adoption of the most effective PB and ABS strategy; and 3) the at least 75% adoption of the most effective ABS strategy. By 2050, Europe could only meet the 1.5 °C target by the simultaneous 100% adoption of the most effective PB and ABS strategies (*SI Appendix*, Fig. S4*C*).

While technically possible, even with transformative agri-food sector actions that remove barriers for the simultaneous 100% adoption of the most effective PB and ABS strategies identified


A Projected change in global emissions between 2012 and 2030 under different scenarios

B Projected change in African emissions between 2012 and 2030 under different scenarios

C Projected change in European emissions between 2012 and 2030 under different scenarios

Fig. 3. Projected change in enteric methane (CH_4) emissions between 2012 and 2030 without mitigation strategy under BAU and modeled mitigation scenarios (Product Based: adoption of one strategy that reduces product-based CH_4 emissions; Absolute: adoption of one strategy that reduces absolute CH_4 emissions; and Product Based & Absolute: adoption of one strategy that reduces product-based CH_4 emissions and one strategy that reduces absolute CH_4 emissions) for enteric CH_4 emission changes globally (*A*), in the African region (*B*), and in the European region (*C*). Error bars represent the average mitigation effect of the least and most effective mitigation strategy. Numbers in squares indicate the percentage of change from BAU.

in this study is unlikely. Consequently, the identified strategies to reduce enteric CH_4 emissions must be enacted together with other measures to decrease CH_4 emissions: For example, strategies to reduce CH_4 emissions from manure handling or pre- or postfarmgate measures, such as the reduction of food waste and a shift to a more plant-based diets (11) when per capita protein consumption is high.

Combining two or more strategies to mitigate enteric CH_4 can increase or decrease the efficacy of the strategies. However, most likely the combination of two or more strategies will give a greater reduction than when only one is used. In this study, it was assumed that the combination of strategies would result in an additive mitigation effect, as this was observed when lipids were combined with tannins (66), 3-NOP (67, 68), or nitrates (69). However, more studies are needed to evaluate the effect of combining two or more strategies, as combinations of multiple mitigation strategies are likely needed to sufficiently mitigate CH_4 to limit global warming to 1.5 °C.

Although one of the identified mitigation scenarios was suited to decrease global enteric CH_4 emissions to limit global warming to 1.5 °C by 2030 but not 2050, the 1.5 °C target is unlikely to be achieved, because 100% of the producers would need to adopt it. While none of the mitigation scenarios would allow Africa to meet the 1.5 °C target, multiple scenarios that did not require a 100% adoption would allow Europe to meet the 1.5 °C target. The reason for this is that Africa had a greater projected BAU increase in enteric CH_4 emissions compared with Europe (87 vs. 11%) between 2012 and 2030, as a result of projected increases in human population (56 vs. 4%) and per capita demand for red meat and milk protein (18 vs. 5%), resulting in a greater absolute increase in demand of red meat and milk protein (84 vs. 9%). In addition, Africa compared with Europe has an overall higher CH_4I_M (104 vs. 19 kg CO_2 equivalents kg milk protein^{-1}) and CH_4I_G (198 vs. 46 kg CO_2 equivalents kg red meat protein^{-1}), which leads to proportionally greater increases in enteric CH_4 for red meat and milk protein produced in Africa compared to Europe. Similar reasons led to the observed differences between 2012 and 2050.

Even though Africa may not be able to meet the 1.5 °C target, the projected BAU per capita red meat and milk protein demand in 2030 will still be 51% and 78% smaller, respectively, than that of Europe (3.4 vs. 6.9 g red meat protein capita^{-1} d^{-1} and 4.3 vs. 19.9 g of milk protein capita^{-1} d^{-1}, respectively). Despite this large disparity in annual animal protein consumption, annual BAU per capita enteric CH_4 emissions for red meat and milk consumed in Africa was 111% and 8% greater, respectively, than that in Europe in 2012 (245 vs. 116 kg CO_2 equivalents capitia^{-1} y^{-1} and 144 vs. 134 kg CO_2 equivalents capita^{-1} head y^{-1}, respectively) and 161% and 25% greater than that in Europe in 2050 (303 vs. 116 kg CO_2 equivalents capita^{-1} y^{-1} and 163 vs. 130 kg CO_2 equivalents capita^{-1} y^{-1}, respectively). This shows the need and opportunity to decrease CH_4I in Africa and other LMIC where CH_4I is high. In Europe and other HIC, where CH_4I and annual per capita enteric CH_4 emissions associated with red meat and milk protein consumption are low but red meat and milk demand are high, emissions might be reduced by shifting demand to plant-based alternatives (11). In addition, red meat and milk exports from HIC to LMIC could help to reduce enteric CH_4 emissions to meet the 1.5 °C target. However, these exports often do not reach food-insecure regions where the money to buy food is limited or unavailable and increases in local production are more likely to meet the demand and recommended levels of dietary protein intake.

Future research needs to: 1) develop novel mitigation strategies, especially for pasture-based systems (less than half of the identified strategies were relevant for pasture systems); 2) increase the understanding of the mitigation potential of combinations of enteric fermentation mitigation strategies; 3) investigate the mitigation effect of identified strategies on emissions of growing and nonlactating cattle (only half of the identified strategies had sufficient data available to evaluate CH_4I_G); 4) estimate offsets of CH_4 mitigation by increases in GHG emissions elsewhere in the supply chain including in longer supply chains characterized by international trade; and 5) identify the barriers to wide-scale adoption of effective mitigation strategies in HIC and LMIC.

Conclusion

This comprehensive meta-analysis identified in a quantitative and comparative manner three effective PB and five effective ABS strategies. The three PB strategies decreased product-based CH_4 emissions by on average 12% (ranging from 9 to 17%) and increased animal production by a median of 17% (ranging from 9 to 162%). The five ABS strategies reduced product-based CH_4 emissions by an average of 17% (ranging from 12 to 32%) and daily CH_4 emissions by an average of 21% (ranging from 12 to 35%). The 100% adoption of only one of the PB or ABS strategies at a time cannot sufficiently decrease global enteric CH_4 emissions from agriculture by 2030 or 2050 to achieve the 1.5 °C target. However, the simultaneous 100% adoption of the most effective PB and ABS strategy can sufficiently decrease global enteric CH_4 emissions to achieve the 1.5 °C target by 2030 but not 2050. Adoption barriers to the identified strategies are likely to prohibit them from reaching their full technical potential. Thus, to ensure meeting the 1.5 °C climate target, it will be crucial that adoption barriers are identified and removed, and the identified strategies are implemented. This also needs to be done for strategies that remove emissions from the supply-and-demand side in the agricultural sector. Furthermore, the mitigation effect of the simultaneous implementation of more than two of the identified strategies should be studied. At a regional level, projected autonomous increases in enteric CH_4 emissions may prevent meeting the 1.5 °C target in studied mitigation scenarios in LMIC, such as for Africa. The projected increases in enteric CH_4 in HIC, such as Europe, are relatively small. Multiple studied scenarios may allow HIC to meet the 1.5 °C target by 2030 and one scenario will also do so for the 2050 target.

Materials and Methods

Literature Search and Classification of Mitigation Strategies. The database for this meta-analysis was compiled using data obtained by searching the databases of the Commonwealth Agricultural Bureau International (CABI), the EBSCO Discovery Service, and the Web of Science. Publications from 1964 through 2016 were searched using CABI and EBSCO Discovery Service with the search terms "rumen" AND "methane" and an additional four searches were completed in the EBSCO Discovery Service using the term "rumen" in combination with "methane," "energy partitioning," "energy metabolism," or "energy balance." Publications from 2017 through 2018 were searched using CABI and Web of Science databases. Seven searches were conducted with the search term "methane" in combination with "beef," "cattle," "dairy," "goat," "sheep," "rumen," or "ruminant" and three searches with the search term "rumen" in combination with "energy balance," "energy metabolism," or "energy partitioning." Publications listed in an independently developed database supported by the AnimalChange project, MitiGate (17), were merged with the database created in the current analysis.

The abstracts of the publications found in the search were reviewed, and based on the abstract content, publications were selected for further consideration if they included in vivo measurement of enteric CH_4 emissions, a clearly defined treatment and control, and multiple replications (at least four or more animals in continuous design experiments, cross-over design experiments, and so forth). Publications were excluded if they were not from peer-reviewed literature or if they were not in English, French, German, Spanish, or Portuguese. Furthermore, publications were excluded if they were based on inappropriate study design (i.e., experimental period ≤10 d) or measurement technique [e.g., the "sniffer technique" that is based on CH_4-to-CO_2 ratio of exhaled breath (70, 71)].

The completed database consisted of 650 publications. From these, only the publications that had a treatment that could be assigned to one of three main mitigation categories, as described below, and reported statistical variance for at least one of the CH_4 emissions emission metrics (e.g., least significant difference, relative standard deviation, or SEM) were included in the final analysis. WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/; accessed 30 October 2019) was used to determine absolute values for a total of nine metrics in seven publications where data were reported as figures.

The data were classified into three main mitigation categories: 1) animal and feed management, 2) diet formulation, and 3) rumen manipulation, each of which was then further classified into up to five subcategories (*SI Appendix*, Table S2). Only the mitigation strategies that each had at least two publications for at least one CH_4 emission metric and two of the remaining CH_4 emission or animal metrics were analyzed within a main category. Treatment effects were assessed relative to their respective control values for all responses; therefore, closely related variables and variables with different units were included in the analysis. For example, CH_4I_M included daily CH_4 emissions per kg of milk and milk corrected for fixed energy, fat and protein, or milk solids (all milk nonwater components combined) content as well as milk solids yield. Similarly, for CH_4I_G, both weight gain and carcass gain were used. Metrics for feed intake included intakes of dry matter, gross energy, organic matter, and intake expressed per unit of body weight or metabolic body weight. Digestibility (of fiber) metrics included only apparent digestibility of neutral detergent fiber. Where multiple treatments of a common treatment type were present within an experiment, the treatment means were averaged, and their respective errors pooled, so that each experiment produced a single "treatment" and "control" pair of response means and SDs.

The final dataset analyzed in the present study included data from 430 peer-reviewed publications, of which 66% were of cattle, 31% of small ruminants (sheep and goats), and 3% of other ruminant species (buffalo, deer, and yak). The complete list of references used in the current analysis is given in *SI Appendix*, Table S1 and the database can be found on https://www.datacommons.psu.edu under the link https://www.datacommons.psu.edu/commonswizard/MetadataDisplay.aspx?Dataset=6333 and the DOI 10.26208/6em7-k817. The majority of the publications reported daily CH_4 emissions (92%), feed intake (84%), and CH_4Y (71%), but less than half of the publications reported weight gain for all animal types (growing, lactating, and other adult animals) (49%), Y_m (48%), fiber digestibility (41%), milk yield (29%), CH_4I_M (21%), or CH_4I_G (7%) (*SI Appendix*, Fig. S5). The final analysis only included weight gain data for growing animals (106 publications), which led to the exclusion of the weight gain data of half of the publications (104 publications) that reported weight gain data for lactating and other adult animals.

Statistical Analysis. A mixed-model meta-analysis weighted by inverse variance was carried out considering treatment mean comparisons within the publications as a random effect. Analyses were run across all ruminant species (cattle, buffalo, deer, goat, sheep, and yak) and included main mitigation strategies and their respective subcategories as potential moderator fixed effects. Analyses were conducted separately for each of the nine response variables (daily CH_4, CH_4Y, Y_m, CH_4I_G, CH_4I_M, feed intake, weight gain for growing animals, milk yield, and fiber digestibility) using a log ratio of means, namely log(treatment/control), in order to standardize treatment effects across multiple measures, species, and outcomes, as well as to allow the expression of treatment differences as relative percentages (72, 73). Weight gain for growing animals when consuming tanniferous plants, however, was assessed based on a standardized relative difference, [(treatment-control)/SE_{Diff}], due to the presence of negative growth rate responses in two treatment mean comparisons (73). Computations were carried out using Comprehensive Meta-Analysis (V. 3.3.070; Biostat). All analyses were adjusted for multiple comparisons using a step-down Bonferroni procedure to reduce the risk of type I error (74) (SAS, v9.4; SAS Institute). The effect of a mitigation strategy was considered significant for adjusted $P < 0.05$ and $0.05 \leq$ adjusted $P \leq 0.10$ was considered as a trend.

Estimation of the Potential for Identified Strategies to Decrease Methane Emissions. The potential of the identified strategies to decrease global, LMIC (e.g., countries in the African region), and HIC (e.g., countries in the European region) enteric CH_4 emissions between 2012 and 2030 and between 2012 and 2050 was estimated using three mitigation scenarios. In the mitigation scenarios, identified measures to mitigate enteric CH_4 from the current analysis (Fig. 2) were applied to demand projections under a BAU scenario. Furthermore, a sensitivity analysis for 100%, 75%, 50%, and 25% adoption rate of mitigation measures was performed.

The BAU scenario was defined by the FAO (75) as a continuation of historical trends of food preferences and inclusion of current initiatives to address sustainable development goal targets. Annual demands for protein from red meat (bovine meat, mutton, and goat meat) and milk for 2012, 2030, and 2050 were projected by using published per capita demand projections by Henchion et al. (64) and human population projections by the FAO (65). Consistent with the demand projections by Henchion et al. (64), projections were classified into the six regions defined by the World Health Organization (WHO; African region, region of the Americas, Southeast Asia region, European region, eastern Mediterranean region, and western Pacific region) (76). The regional production of red meat and dairy protein by production system (feedlot, grassland, and mixed) reported by GLEAM (4) for 2010 was applied to demand projections. As some of the regional classifications in GLEAM differed from the WHO regions, best judgment was used to match GLEAM regions to WHO regions. The countries/regions included in each WHO region in our analysis for demand projections, population projection, and GLEAM are listed in *SI Appendix*, Table S3. Further, CH_4I by animal production system (feedlot, grassland, and mixed) reported by GLEAM for 2010 were multiplied by projected animal protein demand by animal production system to estimate annual enteric CH_4 emissions for each system. For this, the underlying assumption was that demand will be met by increased production in each region.

The three mitigation scenarios were: 1) adoption of one PB strategy (increasing feeding level, decreasing grass maturity, or decreasing dietary forage-to-concentrate ratio); 2) adoption of one ABS strategy (the inclusion of CH_4 inhibitors, tanniferous forages, electron sinks, oils or fats, or oilseeds); and 3) simultaneous adoption of one PB and one ABS.

For a 100% adoption rate of one PB strategy, the identified average (average of all mitigation potentials of strategies applicable to a production system), minimum and maximum (strategies with lowest and highest mitigation potential applicable to a production system, respectively) reductions of CH_4I for a production system were used to adjust the CH_4I reported by GLEAM (4) for red meat and dairy protein for each of the projected years. When there were no data for the CH_4I_G reduction potential of a strategy, it was assumed that the minimum reduction potential was 0%, the maximum reduction potential was the one identified for CH_4I_M, and the average reduction potential was the average of the minimum and maximum reduction potential.

For a 100% adoption rate of one ABS strategy, the identified average, minimum, and maximum reductions of daily CH_4 emission for a production system were used to adjust the projected annual CH_4 emissions for all red meat and dairy protein of a given productions system of the projected years. For a 100% adoption rate of one PB and one ABS strategy, the reduction for the adoption of one PB strategy was first projected, and afterward, the adoption of one ABS strategy was projected. Similar calculations were done for the other three assumed adoption rates (75%, 50%, and 25%).

Data Availability. Data have been deposited in Penn State Data Commons (http://doi.org/10.26208/6em7-k817).

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