

Review: Alternative and novel feeds for ruminants: nutritive value, product quality and environmental aspects

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*Ruminant-based food production faces currently multiple challenges such as environmental emissions, climate change and accelerating food–feed–fuel competition for arable land. Therefore, more sustainable feed production is needed together with the exploitation of novel resources. In addition to numerous food industry (milling, sugar, starch, alcohol or plant oil) side streams already in use, new ones such as vegetable and fruit residues are explored, but their conservation is challenging and production often seasonal. In the temperate zones, lipid-rich camelina (*Camelina sativa*) expeller as an example of oilseed by-products has potential to enrich ruminant milk and meat fat with bioactive trans-11 18:1 and cis-9,trans-11 18:2 fatty acids and mitigate methane emissions. Regardless of the lower methionine content of alternative grain legume protein relative to soya bean meal (*Glycine max*), the lactation performance or the growth of ruminants fed faba beans (*Vicia faba*), peas (*Pisum sativum*) and lupins (*Lupinus sp.*) are comparable. Wood is the most abundant carbohydrate worldwide, but agroforestry approaches in ruminant nutrition are not common in the temperate areas. Untreated wood is poorly utilised by ruminants because of linkages between cellulose and lignin, but the utilisability can be improved by various processing methods. In the tropics, the leaves of fodder trees and shrubs (e.g. cassava (*Manihot esculenta*), *Leucaena sp.*, *Flemingia sp.*) are good protein supplements for ruminants. A food–feed production system integrates the leaves and the by-products of on-farm food production to grass production in ruminant feeding. It can improve animal performance sustainably at smallholder farms. For larger-scale animal production, detoxified *Jatropha* (*Jatropha sp.*) meal is a noteworthy alternative protein source. Globally, the advantages of single-cell protein (bacteria, yeast, fungi, microalgae) and aquatic biomass (seaweed, duckweed) over land crops are the independence of production from arable land and weather. The chemical composition of these feeds varies widely depending on the species and growth conditions. Microalgae have shown good potential both as lipid (e.g. *Schizochytrium sp.*) and protein supplements (e.g. *Spirulina platensis*) for ruminants. To conclude, various novel or underexploited feeds have potential to replace or supplement the traditional crops in ruminant rations. In the short-term, N-fixing grain legumes, oilseeds such as camelina and increased use of food and/or fuel industry by-products have the greatest potential to replace or supplement the traditional crops especially in the temperate zones. In the long-term, microalgae and duckweed of high-yield potential as well as wood industry by-products may become economically competitive feed options worldwide.*

Keywords: legume, by-product, single-cell protein, tree, ruminant

Implications

Within ruminant-based food production, there are potential means to improve global food supply and to decrease its environmental footprint without compromising animal products. Alternative and novel feeds provide opportunities to (a) spare arable land, fresh water (e.g. single-cell proteins

(SCP), duckweed) or fertilisers (N-fixing grain and shrub legumes), (b) exploit side streams more efficiently (residues of food, biofuel or wood production) and (c) increase the use of fibrous feeds not suitable for monogastrics (wood, shrubs). They may also offer additional benefits such as modification of lipids in ruminant products (lupins, camelina, microalgae) and mitigation of methane emissions (lipid-rich feeds, tropical shrubs).

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Introduction

Ruminant-based food production faces currently multiple and global challenges such as needs to respond to the growing human population and food security, but also to the pollution of environment and the accelerating climate change. The animal production sector is also heavily criticised due to food-feed competition, that is, the feeding of human-edible materials to animals and the use of arable land to produce animal feed instead of producing human-edible food directly. Recently increasing interest in biofuel production tightens up the competition on the use of arable land.

Ruminants are often criticised for the lower feed conversion efficiency relative to monogastric livestock, but taking into account differences in the feed rations modifies the ranking order. Indeed, to produce the same amount of animal protein products (meat, milk or eggs) much less human-edible feed is needed in ruminant systems than in monogastric systems (6 v. 16 kg of human-edible feed dry matter (DM) per kilogram of protein products; Mottet *et al.*, 2017). The strengths inherent to ruminant animals in food production chain could be further developed by more diverse and efficient exploitation of side streams and increased exploitation of fibrous feeds not suitable for the nutrition of humans and monogastric livestock. To improve the food system sustainability and to reach climate change targets, changes in feed and animal production alone are not adequate. Changes in food consumption as regard to wastage and balanced dietary choices are also needed (Röös *et al.*, 2017). According to Schader *et al.* (2015), feeding animals solely based on food industry by-products and grasslands combined with changes in human dietary patterns (reductions of animal products) have potential to decrease the environmental load of food production drastically. For example, greenhouse gas emissions, nitrogen (N) and phosphorus (P) load, as well as land and fresh water use could decrease up to 18% to 46%.

Almost half of worldwide bovine milk production takes place in the temperate areas of Europe and Northern America (FAOSTAT, 2016) under intensive (high inputs including concentrate, high milk yield) or extensive production systems (high forage, low inputs, moderate or low milk yield). At the present, the ruminant milk and meat production in Europe relies largely on imported soya bean (*Glycine max*) from South America (Lindberg *et al.*, 2016). Soya bean together with cereals and maize (*Zea mays*), lucerne (*Medicago sativa*) or grass forage are typical dietary ingredients in the intensive farming of the temperate zones. However, the highest cattle populations are in the tropical and subtropical climate zones, the number of cattle in Brazil and India alone comprising 15% and 13% of global cattle population, respectively (FAOSTAT, 2016). In the tropics, the forages are typically of poor nutritive value in terms of low protein and high-fibre content that limits the efficiency of animal production. Local protein sources are thus sought both in the temperate as well as tropical areas.

Enteric methane emissions from ruminants significantly contribute to the environmental footprint of agriculture (Herrero *et al.*, 2016). Ruminal methane production also represents a substantial loss of feed energy. Appropriate forage supplementation and feed choices to improve forage and total diet digestibility have significantly more potential to increase ruminant performance and mitigate methane emissions in the extensive than in the intensive ruminant production systems (Knapp *et al.*, 2014; Herrero *et al.*, 2016). Modern intensive agriculture is a significant source of N emissions as well. Globally, about 50% of the N fertiliser applied to conventional cropping systems is not utilised by plants, but lost to the environment as ammonia (NH₃), nitrate (NO₃⁻) and nitrous oxide (N₂O; Coskun *et al.*, 2017). Legumes with biological N₂ fixation (Watson *et al.*, 2017) may offer an environmentally sound and sustainable nutrient source to ruminants. Furthermore, the N use efficiency of ruminants is mainly determined by diet N content (Huhtanen *et al.*, 2008) indicating the potential to reduce N leakages by dietary N optimisation.

The feasibility of using alternative feeds for ruminants depends among others on the feed value of novel feeds, animal production responses and feed costs compared to the conventional feeds. In addition, the environmental footprint of feed and animal production, and the economic value of novel feeds in alternative uses such as energy production are of great importance. The objective of this article is to review the nutritive value of some currently underutilised or novel feeds for ruminants in the temperate zones (intensive and extensive farming) and in the tropics (extensive farming). In addition, the effects of these feeds on ruminant milk production and quality (milk, protein and fat yields and milk fatty acid composition) as well as meat production (average daily gains (ADG) and meat composition) are examined and compared to more conventional feeds. The environmental load of novel feeds is evaluated based on requirements for arable land and for fresh water during the feed production and their possible effects on methane and nitrogen emissions of ruminants. This review comprises a quantitative evaluation of replacing traditional feeds by alternative ones on ruminant milk production as well as a comparative estimation of time delay for novel feeds to enter readily on the market together with their future potential to increase sustainable production and utilisation in ruminant nutrition.

Intensive and extensive ruminant production in the temperate zones: protein and energy supplements

By-products of food and bioenergy industries

Numerous food and biofuel industry side streams are already used as major components of ruminant diets such as hulls and feed meals from milling industry, distillery and brewery by-products, meals and expellers from plant oil production, molasses and pulps from sugar processing, etc. (Feedipedia, 2018; Luke, 2018). Biofuel by-products as ruminant feeds have been reviewed in detail by Makkar *et al.* (2012). Recent

attempts have aimed at utilising such side streams that have not previously been used. Wadhwa and Bakshi (2013) estimated that nearly 50% of all fruits and vegetables in the European Union go to waste with losses occurring during agricultural production, processing, distribution and by consumers. Vegetable residues may be composted and used as soil amendments but with only a limited added value. One option to add value to these products is to preserve them by sun drying (Wadhwa *et al.*, 2015) or ensiling (Orosz and Davies, 2015) and feed to livestock. Vegetable and fruit residues are challenging raw materials for ensiling as they are easily perishable and typically moist (Wadhwa *et al.*, 2015; Table 1; Supplementary Table S1). Solid-state fermentation of the fruit and vegetable wastes in combination with other non-competing human food biomass could possibly (a) enrich them with proteins and other nutrients, (b) improve feed quality and (c) enhance ensilability (Wadhwa *et al.*, 2015).

The production of fruit and vegetable residues is often seasonal, and in many cases they are produced by small or medium size companies, resulting in rather small batches. To be able to recycle these residues back into the food chain requires high hygienic quality of the products and good stability to allow efficient logistics. Some of the major constraints in the use of fruit wastes are the presence of anti-nutritional factors such as pesticides, mycotoxins, heavy metals and dioxins (Wadhwa *et al.*, 2015). There are, however, positive experiences as, for example, ensiled tomato and olive by-products have been successfully used in the diets of dairy goats (Arco-Pérez *et al.*, 2017) and ensiled apple pomace up to 30% in the diets of lactating dairy cows (Wadhwa *et al.*, 2015).

By-products of oilseed crops such as soya bean and rapeseed meals and expellers are widely used as supplementary protein for dairy cows. One of the less used oilseed crops is an ancient plant camelina (*Camelina sativa*). Camelina has a moderate seed yield potential (Table 2) that combined with low-nutrient requirements and a good resistance to diseases, pests and drought makes it adapted also to low-input farming (Heuzé *et al.*, 2017b). Camelinaseed oil is an economically interesting on-farm raw material for biofuel production (Keske *et al.*, 2013) to increase farmers' energy independence. Camelinaseed oil is also fit for human consumption (Heuzé *et al.*, 2017b). Camelina expeller contains lipids with significant amounts of essential fatty acids 18:2n-6 and 18:3n-3 (Bayat *et al.*, 2015), but it is also relatively abundant in CP and essential amino acids (AA) (Table 1). However, ruminal degradability of camelina protein *in situ* (76%) was higher than that of soya bean (58%) or rapeseed (52%; Lawrence and Anderson, 2015). Feeding unprocessed or processed camelinaseeds to ruminants has sometimes, but not always, decreased DM intake (Table 3; Supplementary Table S2; Table 4; Supplementary Table S3) that may be related to glucosinolates (Lawrence *et al.*, 2016). Nevertheless, replacing various conventional protein feeds in ruminant diets with camelina expeller has resulted in comparable milk and protein yields (Table 3) or ADG (Table 4).

Feeding camelina expeller results in high concentrations of *trans*-11 18:1 and *cis*-9,*trans*-11 18:2, unaltered or slightly decreased 18:0 and *cis*-9 18:1 concentrations and a significant decrease in total saturated fatty acids in dairy cow (Halmemies-Beauchet-Filleau *et al.*, 2011 and 2017), in sheep (Szumacher-Strabel *et al.*, 2011) and in goat milk (Cais-Sokolińska *et al.*, 2015) as well as in sheep meat (Table 4). Besides beneficially modifying lipids in ruminant milk and meat, camelina lipids at inclusion rate of 6% in the diet DM decreased ruminal methane and carbon dioxide production of dairy cows by 29% and 34%, respectively (Bayat *et al.*, 2015). However, caution should be exercised in the dosage of lipids as the reduction in methane emissions due to the dietary polyunsaturates may be accompanied with lowered DM intake and milk yield (Bayat *et al.*, 2015).

Grain legume seeds

Grain legumes such as faba bean (*Vicia faba*), pea (*Pisum sativum*) and lupins (*Lupinus* sp.) are old crops cultivated in all arable continents. There are three major modern lupine species bred to animal feed namely white (*Lupinus albus*), blue (*Lupinus angustifolius*) and yellow lupin (*Lupinus luteus*). In the short-term, grain legumes are presumably the most promising alternatives to soya bean (*Glycine max*) and rapeseed in the temperate areas because their cultivation practices are already available and implemented (Figure 1). However, grain legume seeds are edible by humans as well. Therefore, the utilisation of human-inedible feeds for ruminants and/or feeds the production of which require less or not at all arable land should be encouraged to improve further the sustainability of food production system in the longer term.

The unique capacity of leguminous plants in conjunction with rhizobium symbionts to biologically fix and utilise atmospheric N enables that inorganic N-fertilisers with rising prices and high requirement of energy in manufacturing are not required. Indeed, the emissions of a potent greenhouse gas N₂O from legume cultivation are generally lower than those from N-fertilised crops (1.3 v. 3.2 kg/ha; Watson *et al.*, 2017). The seed yield potential of grain legumes under optimal conditions is similar or exceeding that of conventional protein crops (Table 2). These advantages make legumes increasingly attractive in the intensive farming in addition to current wide spread use in the low-input and organic farming.

A prerequisite for the spread of grain legume production is the profitability relative to other crops. This is influenced, for example, by yields, volatile producer prices, incentives and production costs. Though the producer prices of grain legume seeds are on average 1.1 to 2.0 times higher than that of wheat in Europe (FAOSTAT, 2016), the competitiveness against more common crops such as wheat is uncertain mainly due to inconsistent DM yields and high seed costs. However, the incentives for protein feeds and reducing the seed costs by producing the seed on-farm can improve the competitiveness of grain legume cultivation. The cultivation

Table 1 Chemical composition of some alternative and common feeds for ruminants

Feed ¹	DM g/kg	Ash	NDF	Starch	EE	CP	His	Met	Lys
		g/kg DM				g/kg CP			
Common protein feeds									
Rapeseed expeller	899	69	299		92	391	28	22	56
Soya bean expeller	907	68	111		77	493	27	14	63
By-products of food industry									
Apple pomace	360	26	525		50	77			
Camelina seed expeller	905	69	305	2	156	357	23	20	46
Cauliflower leaf	654	162	145			126			
Cucumber waste	37	113	168			163			
Grape marc	876	63	658		64	115	29	15	45
Tomato fruit waste	62	101	191			103			
Olivesilage (pulp + leaf)	575	127	390			88			
Grain legume seeds									
Faba bean	866	39	159	447	14	290	26	8	62
Lupin, blue	915	42	253	122	63	332	28	7	50
Lupin, white	912	43	235	84	105	344	23	8	50
Lupin, yellow	898	54	254	35	53	435	27	7	50
Pea	865	35	142	513	12	239	25	10	72
Soya bean	887	57	132	64	214	396	26	14	62
Grass silage juice	98	193				190			
Grain legume whole crop stands									
Faba bean	168	62	387	82		175			
Lupin, white	142	68	395			169			
Pea	198	65	397	67		167			
Trees or shrubs (leaves unless otherwise stated)									
Cassava	250	126	459			223		46 ²	
Flemingia	290	53	531			258		58 ²	
Leucaena	320	64	316			205		36 ²	
Moringa	330	115	219		54	251	31	21	66
Pine bark		22	667		47	28			
Sesbania	290	103	258			233			
Willow	264	71	573			167			
Jatropha kernel meal, detoxified	876 to 971	79 to 136	98 to 200	68 to 120	4 to 52	624 to 775	27 to 33	14 to 17	30 to 36
Single-cell protein									
Bacteria		30 to 70			10 to 30	500 to 650	23	30	61
Fungi		90 to 140			20 to 80	300 to 450	15 to 20	15 to 17	38 to 61
Microalgae									
<i>Chlorella vulgaris</i>	946	57	0	43	95	608	18	19	49
<i>Euglena gracilis</i>	960	35	0		138	240	26	20	66
<i>Scenedesmus obliquus</i>		60 to 100			120 to 140	500 to 600	15 to 17	12 to 21	50 to 57
<i>Schizochytrium</i> sp.		82	6 ³		380 to 710	121	8	< 8	33
<i>Spirulina platensis</i>	940	70	0	64	55	692	16	22	39
Yeast		50 to 100			20 to 60	450 to 550	21 to 22	13 to 21	74 to 77
Seaweed									
<i>Ascophyllum nodosum</i>	100 to 300	225	209		39	80	14	13	46
<i>Macrocystis pyrifera</i>	100 to 300	320	199		6	101	13	19	47
<i>Ulva</i> spp.	100 to 300	230	262		12	186	20	16	38
Duckweed	56	159	401		61	291	17	8	39

EE = ether extract.

¹References in Supplementary Table S1.²Tannins g/kg dry matter (DM).³Crude fibre.

of grain legumes is more challenging than that of cereals and grasses as they are sensitive to lodging and due to pests and pathogens they require efficient crop rotation (van Krimpen *et al.*, 2013). Nevertheless, the plant breeding may be able to

overcome these agronomical constraints if given enough attention and resources.

Grain legume seeds differ in the chemical composition, the CP content ranging from 240 (peas) to 400 g/kg DM (soya beans).

Table 2 The suitability for local production of some common and alternative feeds in different production systems, potential yields in Europe, the need of land or water for feed production, and other main environmental aspects regarding crop and ruminant production

Feed	Local production			Yield ¹ (t/ha)		Need for		
	TInt	TExt	Tropics	DM	N	Land	Fresh water	Other environmental aspects
Common feeds								
Rapeseeds	Yes	Yes		1.5 to 3	0.6 to 1.2	Arable	High	Need for N fertilisation to get high yields ¹
Soya beans	Yes	Yes	Yes	3	0.8	Arable	High	Legume, but day length and temperature restricts yield potential and expansion to northern periphery ¹
Wheat	Yes	Yes	(Yes)	10	1.1	Arable	High	Need for N fertilisation to get high yields
Grass forage	Yes	Yes	(Yes)	10 to 15	1.2 to 2	Arable	High	Need for N fertilisation to get high yields, or inclusion of forage legumes
Alternative feeds								
Camelina seeds	Yes	Yes		3	0.8	Arable	High	Modest needs for cultivation compared to rapeseed Polyunsaturates of Camelina lipid may decrease ruminal methane emissions ²
Legume grains peas, beans, lupins	Yes	Yes	(Yes)	4 to 6	1 to 2	Arable	High	Legumes, therefore no need for N fertilisation. High ruminal degradability of protein and unbalanced amino acid profile of undegradable protein may increase N emissions from ruminants ³
Legume forage	Yes	Yes		13	2.5	Arable	High	Legumes, therefore no need for N fertilisation. Due to lower fibre content, legume forages may mitigate ruminal methane emissions
Hemicellulose		Yes	Yes			Forest	High	Low in N and P. Incorporation in the diet may improve N and P use efficiency if basal diet is excessive in these nutrients
Leaves (tropical trees and shrubs)			Yes			Forest	High	Secondary compounds in certain species may direct rumen fermentation towards propionate and thus mitigate methane ⁴
Jatropha fruit			Yes	2.5 to 5 ⁵	1.7 to 3.4 ⁵	Arable Forest	High	Decrease soil erodibility due to lateral roots. ⁵ Utilisation of jatropha kernel meal that is a by-product of oil extraction as animal feed improves overall nutrient recycling
Single-cell protein excluding microalgae	Yes	Yes	Yes			No	Low	Can recover nutrients from wastewaters and transform low-value organic by-products to feed
Microalgae	Yes	Yes	Yes	15 to 30	4 to 15	No	Low	Can recover nutrients from wastewaters. Based on chemical composition, species rich in lipids and low in fibre may have potential to mitigate ruminal methane emissions. Ruminal protein metabolism warrants further research
Seaweed		(Yes)	(Yes)	25	2.5 to 7.5	No	No	Harvesting in the wild decreases nutrient loading of marine environment, but effective cultivation and harvesting may impair the equilibrium of coastal ecosystems ⁶
Duckweed	Yes	Yes	Yes	30 to 40	10 to 18	No	Low	Can recover nutrients from wastewaters

TInt = intensive temperate production; TExt = extensive temperate production; DM = dry matter; Yes = suitable; (Yes) = suitable with some restrictions such as species or cultivars (pulses, grass and wheat) or the proximity of the seaside (seaweed).

¹Van Krimpen *et al.* (2013).

²Bayat *et al.* (2015).

³Watson *et al.* (2017).

⁴Table 5.

⁵Yield potential in tropical areas; Heuzé *et al.* (2016b).

⁶Makkar *et al.* (2016).

Soya beans have in general the highest ether extract (EE) content, whereas faba beans and peas contain significant amounts of starch and lupin seeds NDF (Table 1). The main storage carbohydrate of lupins is pectin instead of starch (White *et al.*, 2007). Lupin seeds contain more EE than faba beans and peas

(Table 1) with *cis*-9 18:1 and 18:2n-6 as major fatty acids (White *et al.*, 2007). The protein in grain legume seeds, faba beans and lupin seeds in particular, is low in methionine (Table 1), which is often the limiting AA for the lactation performance of dairy cows (e.g. Pisulewski *et al.*, 1996).

Table 3 The effect of some alternative protein feeds on milk production of ruminants

Species	Alternative protein feed	Control protein feed	SR ¹ (%)	Diet DMI (%)	Milk yield in control (kg/day)	Yield (%) ²					N ³	Ref. ⁴	
						Milk	Lactose	Fat	Protein	Milk urea (%)			
Cow	Camelina E	RSM	100	-3	31	4	4	-3	1	-16	1	1	
	Faba bean	RSM	50	-3	31 to 32	-2	-2	0	-4	7	2	2	
	Faba bean	RSM	100	-4	25 to 35	-6	-5	-2	-7	13	5	2 to 5	
	Faba bean	SBM	40	-1 ⁵	20 to 22	0	1	-3	-1	-10	2	6	
	Faba bean	SBM	100	-1	27	0	1	-3	-1	-10	1	7	
	Lupin, blue	RSM	50	-1	31	-4	-3	0	-2	-5	1	8	
	Lupin, blue	RSM	100	-4	31 to 35	-6	-3	2	-6	2	2	4,8	
	Lupin, white	SBM	100	-1	26 to 38	0	1	-1	-3	3	5	9 to 11	
	Lupin, yellow	SBM	100	-5	32	-6	-5	0	-9	nr ⁶	1	12	
	Pea	RSM	50	-1	24	-2	-2	1	-3	2	1	13	
	Pea	RSM	100	-3	24 to 25	-6	-6	-5	-7	12	2	5,13	
	Pea	RSM-SBM	95	nr	32	-5	nr	6	-2	nr	1	14	
	Pea	SBM	33 to 80	4	21 to 35	2	3	3	4	17	5	15 to 17	
	Pea	SBM	100	2	21 to 27	2	3	1	3	-2	2	15,18	
	Microalgae	RSM	50	-1	23 to 31	0	-1	-1	2	4	3	3,19	
	Microalgae	RSM	100	0	23 to 28	-3	-2	-2	-1	3	2	19	
	Microalgae	SBM	100	0	30	4	4	11	4	-8	3	20	
	Sheep	Camelina E	RSM	50 to 60	nr	1.2	11	-1	-6	-2	nr	2	21,23
		Camelina E	RSM	100	nr	1.2	8	-1	-14	-1	nr	1	21
Camelina S		SBM	50	-2	0.7 to 0.8	7	8	11	6	nr	2	23	
Faba bean		SBM	100	2	0.7 to 0.8	-1	2	-1	2	nr	2	24,25	
Lupin, white		SBM	100	-5	1.4	5	8	3	1	-2	1	26	
Pea		SBM	100	-2	0.7 to 0.8	9	12	7	4	-2	2	24,25	
Pea		SBS-SFM	100	-5	1.0	4	3	6	8	nr	1	27	
Goat	Faba bean	CS	100	0	1.1	-2	-11	-11	0	nr	1	28	
	Faba bean	WLS	100	3	1.6	1	-2	-3	0	nr	1	29	

E = expeller; S = seed; DMI = dry matter intake; CS = cottonseeds; RSM = rapeseed meal; SBM = soya bean meal; SBS = soya bean seeds; SFM = sunflowerseed meal; WLS = white lupin seeds.

¹Isonitrogenous substitution rate (SR) of control protein feed by alternative protein feed.

²Change (%) due to alternative protein feed compared to control protein feed.

³Number of diet comparisons.

⁴References shown in Supplementary Table S2.

⁵Concentrate intake.

⁶Not reported.

The feasibility of the use of alternative grain legumes in ruminant diets is determined not only by their chemical composition, but also by the rate and extent of degradation of nutrients in the rumen. The degradability of faba bean, pea and lupin protein in the rumen is often over 80% (Watson *et al.*, 2017) that is significantly higher than those of soya bean or rapeseed expellers. In addition, the heat-treatment of faba beans, peas or lupin seeds to lower ruminal degradability has seldom improved animal performance (White *et al.*, 2007; Watson *et al.*, 2017). It is plausible that the high-protein degradability in the rumen together with suboptimal AA profile in the undegraded protein of alternative grain legume seeds limit their production responses in high-yielding ruminants. Faba beans contain also antinutritional factors such as vicine and convicine (Heuzé *et al.*, 2016a), lupins quinolizidine alkaloids (Wasilewko and Buraczewska, 1999) and peas lectins and tannins (Heuzé *et al.*, 2017a). However, ruminants are not susceptible to most of

them because of microbial metabolism and degradation in the rumen (Watson *et al.*, 2017).

Replacing protein in soya bean meal partially or completely with faba beans, blue lupin, white lupin or peas has resulted in rather similar bovine lactation performances (Watson *et al.*, 2017; Table 3). Furthermore, the milk fat concentration of medium chain saturates has been lower and those of *cis*-9 18:1 and 18:2n-6 higher in cows fed white lupins seeds relative to soya bean meal (White *et al.*, 2007). In contrast, the milk production responses of alternative grain legumes are often inferior compared to the rapeseed meal in dairy cow nutrition (Watson *et al.*, 2017; Table 3). Substitution of rapeseed meal with faba beans has typically decreased milk protein yield and increased milk urea concentration and the proportion of N excreted in urine suggesting less efficient use of protein in faba beans than in rapeseed (Puhakka *et al.*, 2016; Table 3), thus leading to increased N emissions from animals.

Table 4 The effect of some alternative feeds on the average daily gains (ADG) of ruminants

Species	Alternative feed	Control feed	SR ¹ (%)	Diet DMI ²	ADG ²	Main findings	Ref. ³
Beef steers	Camelina meal	Soya bean meal	100	Dec	–	Camelina increased plasma 18:3n-3 concentration and lessened the acute-phase protein reaction	1
Dairy heifers	Camelina meal	Linseed meal	100	–	–	Camelina decreased plasma insulin concentration. Camelina had no major effect on CP or NDF total tract digestibility or rumen fermentation except for higher ammonia relative to other treatments	2
		Distillers dried grains with solubles	100	–	–		
Sheep	Camelina expeller	Rapeseed meal	50	nr	nr	Camelina increased muscle ω 11 18:1, ω 9 11 18:2 and n-3 fatty acid content, but had no effect on 18:0 or ω 9 18:1	3
Beef bulls	Lupin (blue) seeds	Rapeseed meal	100	Dec	Dec	Carcass weight and dressing percentage were the highest for rapeseed. Protein source had no effect on carcass classification or gross chemical composition. Muscle fatty acid profile was similar for lupin and soya bean diets, but on rapeseed diet muscle ω 9 11 18:2 and 18:3n-3 contents were higher	4
		Soya bean meal	100	–	–		
Beef bulls	Lupin (white) seeds	Soya bean seeds and meal	100	–	–	Main slaughtering and sectioning characteristics were equal. Lupin diet reduced fatness. Quality traits of meats were comparable in terms of colour, tenderness and chemical and fatty acid profile as well as post slaughtering pH	5
Beef bulls	Faba bean-cereal silage Pea-cereal silage	Grass silage	100	–	–	Replacing grass silage with grain legume-cereal whole crop silages had no remarkable effect on carcass characteristics, meat quality, fatty acid profile or sensory score	6
		Grass silage	100	–	–		
Beef steers	Lupin (white) silage	Grass silage	100	–	–	Carcass merits were equal. Lupin nitrogen degraded faster in the rumen compared to grass	7
Sheep	Faba beans Lupin (white) seeds	Soya bean expeller	100	Dec	–	Protein source had no effect on carcass characteristics except for decreased back fat thickness for faba bean	8
		Rapeseed meal	100	–	–		
Sheep	Lupin (white) seeds	Rapeseed meal	100	–	–	Digestibility of CP and energy were higher for lupin than rapeseed and soya bean	9
Sheep	Peas	Soya bean meal	100	–	–	Carcass and meat composition and quality were not affected by treatments	10
		Soya bean meal	45	–	–		
Sheep	Pea silage	Grass silage	100	–	–	Lambs offered pea silage low in tannins grew faster, had increased chop length and improved digestibility of OM and N compared to grass silage as sole forage in the diet	11
Sheep	Seaweed	Soya bean–barley concentrate	20	–	–	Replacing 20% of soya bean–barley concentrate with seaweeds (<i>Ruppia maritima</i> or <i>Chaetomorpha linum</i>) had no effect on OM or CP digestibility, nitrogen partitioning or water intake	12
Sheep	Seaweed	Alfalfa hay	8	–	–	Dietary supplementation of seaweed (<i>Ulva lactuca</i>) at low level has no adverse effect on growth of sheep	13
			13	–	–		
Goat	Jatropha kernel expeller	Soya bean expeller	50	Inc	Inc	Replacing 50% or 100% of soya bean expeller with fungally detoxified jatropha kernel expeller had no adverse effects on blood parameters. Diet with 1 : 1 (w/w) soya bean expeller and jatropha kernel expeller resulted in highest DM and CP intake and ADG	14
			100	–	–		
Sheep	Jatropha expeller	Soya bean meal	70	–	–	Replacing 70% of soya bean meal in concentrate mixture had no adverse effects on DM intake or ADG of male lambs. The fertility of rams was slightly improved by jatropha inclusion in the diet	15

OM = organic matter.

¹Substitution rate of control feed by alternative feed.

²Effect of alternative feed on dry matter intake (DMI) or ADG: Dec = decrease; – = no effect; Inc = increase; nr = not reported.

³References shown in Supplementary Table S3.

Partial or total replacement of soya bean or rapeseed protein by faba beans, lupin seeds or peas has not significantly altered ADG or meat chemical composition in growing sheep or cattle (Table 4). Besides replacing protein in ruminant diets, starchy faba beans and peas (Table 1) and lupins with higher metabolisable energy content than cereals (Watson *et al.*, 2017) have potential in replacing cereals as well. Indeed, the substitution of cereal grains by grain legumes in dairy cow diets generally increases milk production (White *et al.*, 2007; Watson *et al.*, 2017). Furthermore, starch in peas and faba beans has lower degradability in the rumen than cereal starch (Watson *et al.*, 2017) that lowers the risk for acidosis.

Biorefining of forage crops

Interest in using grass biomass as a raw material for green biorefineries has arisen recently (McEniry and O'Kiely, 2014; Hermansen *et al.*, 2017). Grass is effective in converting solar radiation into chemical forms of energy and it grows well in humid temperate areas with a capacity for higher biomass and CP production compared to most annual crops (Table 2).

Further, existing technology is available for its cultivation, harvesting and ensiling (Wilkinson and Rinne, 2018). When preserved as silage, the grass biomass can be refined all year round although losses in the protein and water soluble carbohydrates will take place during the fermentation process compared to the parent herbage.

Typically the first step in a green biorefinery process is liquid–solid separation resulting in a liquid fraction containing the soluble components of grass and a fibrous solid fraction. The yield of the fractions depends on the technical solutions of the process, but it is also greatly affected by the raw material characteristics. The ensiling process can even serve as a pretreatment for the biorefinery process, and it may be further improved by using fibrolytic enzymes at the time of harvest as it has increased the liquid yield (Rinne *et al.*, 2017). In the simplest approach, grass juice can be used as a liquid feed to enrich the diet with highly nutritive forage-based component and it is readily consumed by dairy cows and monogastric animals (Rinne *et al.*, 2018), or the fibre fraction can be used as a feed for ruminants (Savonen *et al.*, 2018). Grass fibre is less lignified than, for example,

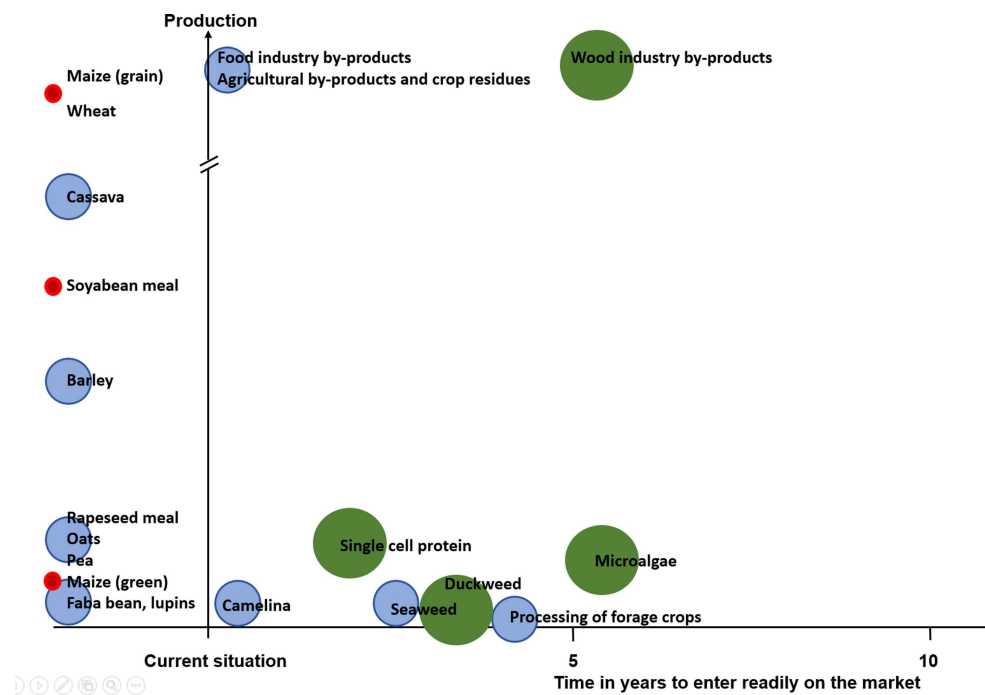


Figure 1 Rough overview of some feeds for ruminants with respect to time to enter readily on the market, extent of production today and potential to increase utilisation in ruminant nutrition sustainably in future (small red bubble = limited; medium-sized blue bubble = moderate; large green bubble = high). Data adapted in part from FAOSTAT (2016), Kruus and Hakala (2016) and USDA (2016).

woods and straw, and milder processes can be used to hydrolyse it (Niemi *et al.*, 2017). The hydrolysed sugars can further be used for a variety of purposes including direct use as feeds, and as substrates for lactic acid fermentation or SCP production. Green biorefineries have potential to improve local nutrient self-sufficiency, provide new business opportunities for rural communities and to produce ecosystem services such as improved soil structure, carbon sequestration and biodiversity. The high costs related to transportation and processing have to date prevented the development of commercial green biorefineries on a large scale (Xiu and Shahbazi, 2015).

Intensive and extensive ruminant production in the temperate zones: fibrous feeds

Grain legumes as forage

Harvesting grain legume stands as whole crop silage enables the utilisation of nutrients in stems and leaves as well and extending the cultivation in areas where the length of growing season may limit complete seed ripening. Although yield potential and organic matter digestibility (OMD) of grain legume stands are high (Rinne *et al.*, 2014; Table 2), data on the effects of grain legume whole crop silages on ruminant performance and product quality is limited. In milk production, white lupin silage resulted in lower total DM intakes, but almost similar bovine lactation performance to maize silage as basal forage (Kochapakdee *et al.*, 2004). In meat production, animal performance has been similar or better when white lupin or pea silages have replaced partially or completely grass silage in cattle or sheep diets

(Table 4). Due to their lower fibre concentration relative to grass silage, legume silages may lower ruminal methane emissions (Hristov *et al.*, 2013).

Compared to sole cropping, the bi-cropping of grain legumes and cereals may enhance and stabilise DM yields, reduce weeds and plant diseases and improve N-fixation (Hauggaard-Nielsen *et al.*, 2008). As a forage, grain legume–cereal crop mixtures complement the nutritive value of each other providing an appropriate balance between readily fermentable nutrients and N in the rumen (Watson *et al.*, 2017). Replacing half of the grass silage DM with faba bean–wheat silage had no effect on DM intake or bovine milk, fat and protein yields or feed N conversion efficiency to milk protein (Lamminen *et al.*, 2015). Whole crop faba bean–wheat or pea–wheat silages have successfully replaced grass silage in beef production as well (Table 4). Due to the lower costs of N fertilisers and good yield potential, grain legume silages seem to provide a viable alternative for maize and grass silages both in the intensive and extensive production systems (Table 2). The feeding value and ruminal methane emissions of diets containing forage legumes (lucerne, clovers) have been reviewed elsewhere (Dewhurst, 2013).

Temperate wood-derived products

Wood is the most abundant source of carbohydrates worldwide. Principal components of wood are cellulose (400 to 450 g/kg DM) and hemicelluloses (200 to 300 g/kg DM, Sjöström, 1993). Agroforestry approaches in ruminant nutrition are less common in the temperate areas compared to the tropics or the Mediterranean area. There are, however,

some applications where, for example, willow (*Salix* sp.) production for wood chips and the grazing of ruminants are combined to provide additional benefits such as improved microclimate for the animals, self-medication and soil carbon sequestration, although the potential of the untreated wood-based materials to provide energy and nutrients to high-yielding dairy cows is limited (Smith *et al.*, 2012 and 2014). Indeed, the *in vitro* digestibility of DM of untreated wood of various tree species was poor with a range from 0.002 to 0.035 (Millett *et al.*, 1970).

A variety of technologies have been used over decades to improve the digestibility of wood-derived ligno-cellulosic materials. The key is to break the link between the lignin and the cell wall carbohydrates, particularly hemicelluloses, in order to improve the digestibility of ligno-cellulose by rumen microbes. Most pulping and papermaking residues have undergone at least partial delignification. Depending on the process, the residue may contain different proportions of hemicellulose and/or cellulose with or without lignin. The digestibility of pure cellulose is rather high and corresponds to the digestibility of typical ruminant feeds such as cereal grains and good quality forages. Saarinen *et al.* (1959) determined the *in vivo* digestibility of 40 wood pulps produced by various pulping methods and reported a range in digestibility from 0.27 to 0.90 depending on the lignin content. The *in vivo* digestibility of bleached (lignin erased and the pulp whitened) chemical pulp fines from mixed hardwood was 0.78 for DM and 0.86 for carbohydrates (Millett *et al.*, 1973), indicating that the materials have a high energy value for ruminants.

Although wood-derived cellulose can be used as a feed for ruminants, it has higher value as, for example, paper raw material. In contrast, hemicelluloses are a by-product of pulping that are typically burned, and interest of using them as feeds has arisen. Hemicelluloses are not homogeneous compounds but a group of mixed polysaccharides. They can be divided into four groups according to their main type of sugars: xylans, xyloglucans, mannans and β -glucans. Spruce (*Picea* sp.) and pine (*Pinus* sp.; softwood) contain somewhat less hemicelluloses than birch (*Betula* sp.; hardwood) and hemicellulose composition differs between species (Saarinen *et al.*, 1959). Glucmannans and galactomannans are the

principal hemicelluloses of coniferous trees (spruce and pine) and xylans in deciduous trees (birch) while β -glucans are restricted to grasses.

Hemicelluloses in a liquid form are often called wood molasses or wood sugar concentrates. They have successfully been used as diet components for ruminants at up to 10% of DM intake (Zinn *et al.*, 1990 and 1993; Herrick *et al.*, 2012). An *in vitro* gas production experiment revealed that hot water and pressure extracted galactoglucomannan and xylan were readily used as fermentation substrates by rumen microbes of dairy cows fed a grass silage and cereal based diet but arabinogalactan was not (Rinne *et al.*, 2016). In an *in vivo* digestibility trial, the OMD of the hot water and pressure extracted galactoglucomannan was 0.591 (Rinne *et al.*, 2016).

Bark is another component of wood that has limited value in the pulp and sawmill industry. Although wild ruminants consume bark voluntarily, the energy value of it is so low that incorporating it into dairy cow diets resulted in the reduction of milk production (P. Kairenius *et al.*, unpublished results). Thus, some processing would be needed to improve the digestibility of bark. Wood-derived feeds typically have very low N and P concentrations. If the basal diet were high in these nutrients, wood-derived feeds could dilute diets and subsequently increase, for example, the N use efficiency of lactating dairy cows as it is mainly determined by N intake (Huhtanen *et al.*, 2008). Wood-derived feeds may also provide a source of feed in the case of lack of other feeds, for example, in crisis situations. In general, they may fit best in the diets of animals with low-energy requirements rather than in dairy cow diets in the intensive production systems.

Extensive ruminant production in the tropics: protein supplements

Fodder trees and shrubs

Low-quality forages such as rice (*Oryza sativa*) straw and pangola (*Digitaria eriantha*) grass low in protein and high in NDF and ADF are common in ruminant nutrition in the tropics (42, 691 and 424 g/kg DM for rice straw (Heuzé and Tran, 2015b) and 5 to 12, 610 to 790 and 350 to 420 g/kg DM for pangola grass (Tikam *et al.*, 2013), respectively). Thus, the

Table 5 Effect of using tropical fodder tree and shrubs supplementation on feed intake, rumen volatile fatty acid production and milk yield in ruminants fed rice straw based diets

Supplement	Form	Dose (kg/day)	Species	DM intake	Rumen fermentation				Milk yield	Ref. ¹
					TVFA	C ₂	C ₃	C ₄		
Cassava	Hay	2.0	Dairy cow	Inc	Inc	Dec	Inc	Dec	Inc	1
	Silage	2.5	Dairy cow	Inc	Inc	Dec	Inc	–	Inc	2
Leucaena	Silage	RLS60	Dairy steer	Inc	Inc	Dec	Inc	–	–	3
	Hay	6.0	Buffaloes	–	Inc	Dec	Inc	–	–	4
Flemingia	Hay	FHM + CH	Dairy steer	–	–	Dec	Inc	Dec	–	5

DM = dry matter; TVFA = total volatile fatty acids; C₂ = acetate; C₃ = propionate; C₄ = butyrate; Dec = decrease; – = no effect; Inc = increase; RLS60 = 40% rice straw + 60% leucaena silage fed *ad libitum*; FHM + CH = 75 g flemingia hay meal + 75 g cassava hay.

¹References shown in Supplementary Table S5

basal diet is typically much lower in protein and higher in fibre compared to that used in the intensive ruminant production of the temperate zones. In Asian tropics, rice straw is commonly supplemented with cassava (*Manihot esculenta*) chip rich in soluble carbohydrates but poor in CP (750 to 850 g/kg DM and 20 to 30 g/kg DM, respectively; Wanapat and Kang, 2015) and soya bean meal. However, the high price of soya bean meal limits its use in smallholder farming.

Leaves of local fodder trees and shrubs such as cassava, leucaena (*Leucaena leucocephala*), moringa (*Moringa oleifera*) and sesbania (*Sesbania sesban*) often contain almost as much CP as NDF (Table 1), the concentration of former being roughly half of that in soya bean meal. Supplementing the rice straw-based diets with these alternative protein sources increases DM intake, improves microbial protein synthesis in the rumen and the efficiency of rumen fermentation with a shift towards propionate (Table 5; Supplementary Table S4), thus potentially mitigating methane production. These beneficial changes may be due to certain natural secondary compounds present in these alternative feeds, namely condensed tannins and saponins (Wanapat *et al.*, 2013).

Combined food–feed production system to provide a year round feeding calendar and to enrich smallholder farming environment is illustrated in Supplementary Figure S1. Under the proposed system, two grass types with (a) erect and tall growth habit and (b) semi-prostrate or prostrate growth habit are used to maximise the biomass production under zero-grazing and grazing, respectively. Roots from cassava can be utilised as a carbohydrate source while the whole top is dried to provide protein (Wanapat, 2009; Wanapat *et al.*, 2017). In addition, the leaves of fodder trees and shrubs such as leguminous leucaena, Flemingia (*Flemingia macrophylla*), and moringa are harvested in intervals and used fresh or preserved for later use. The intercropping of cassava with leguminous crops, for example, common bean (*Phaseolus calcaratus*) and cowpea (*Vigna unguiculata*), has potential to improve soil fertility and to increase biomass yield (Wanapat, 2009; Wanapat *et al.*, 2017). Crop residues such as rice straw, corn stover and sugar cane top are also exploited in ruminant feeding.

Jatrophas

Jatrophas are drought-resistant shrubs or small trees native to American tropics and widely distributed in the tropical and subtropical regions around the world. *Jatropha* genus includes more than 175 species, *Jatropha curcas* being one of the most studied species in animal feeding. *Jatropha* is an interesting biofuel crop due to the high EE concentration of its kernels (570 to 600 g/kg DM; Makkar *et al.*, 2012), and the de-fatted kernel residue, *jatropha* kernel meal, is a good source of nutrients with CP concentration of 620 to 770 g/kg DM (Table 1). In comparison to soya bean protein, *jatropha* is deficient in lysine, but richer in other essential AA (Table 1; Makkar *et al.*, 2012).

The majority of *jatropha* species are highly toxic to both ruminants and monogastrics due to phorbol esters (1 to 3 mg/g kernel meal; Makkar *et al.*, 2012), but they can

successfully be detoxified. The complete detoxification is absolutely necessary to avoid animal mortality (Elangovan *et al.*, 2013). In addition, the high concentration of anti-nutritional factors (trypsin inhibitors, lectin and phytate) may limit the use of *jatropha* especially for monogastrics unless deactivated by heat treatment and supplemented with phytase enzyme. When completely detoxified, the substitution of soya bean by *jatropha* has not impaired the DM intake or ADG of sheep and goats (Table 4). Though the yield potential is high (Table 2), the inconsistency of yields of current cultivars is the major restriction for the spread (Heuzé *et al.*, 2016b).

All production systems of ruminants worldwide: alternative protein and fibrous feeds

The major advantages of SCP, seaweed and duckweed are the independence of production from arable land and of weather conditions as well as the high and continuous harvests (Nasseri *et al.*, 2011; van der Spiegel *et al.*, 2013; Table 2). However, cultivation, harvesting, preservation (especially drying) and application in feed in a large scale needs further research (van Krimpen *et al.*, 2013) to lower the production cost of these novel feeds to competitive level. In the long-term, microalgae and duckweed have perhaps the greatest potential to become viable local protein and fibre sources for ruminants worldwide (Table 2; Figure 1).

Single-cell protein

Single-cell protein consists of microbial cells from yeast, bacteria, fungi or microalgae. These micro-organisms can utilise a wide variety of inexpensive feedstocks and wastes as sources of carbon, nutrients and energy for growth to produce biomass rich in protein. The protein content of SCP varies due to culture conditions, species and strains (Lindberg *et al.*, 2016) but is in the same order as in soya bean expeller (Table 1). The major constraints are the risk for allergens and the accumulation of heavy metals, pesticides and toxins especially if grown on polluted and contaminated substrates, generally high-nucleic acid content (bacteria and yeasts > fungi > microalgae; 60 to 120, 70 to 100, 30 to 80 g/kg DM, respectively) and economical and efficient mass-scale production and harvesting (Nasseri *et al.*, 2011; Lindberg *et al.*, 2016). Dietary nucleic acids and their derivatives are rapidly degraded in the rumen and certain end-products can be re-used as sources of carbon and N for bacterial growth (McAllan, 1982), but the N in nucleic acids is not as easily available as that of true protein or ammonia.

The basic stages of SCP production process include (a) medium preparation, (b) fermentation or photosynthesis and (c) harvesting and downstream processing like washing, cell disruption, protein extraction and purification (Ravindra, 2000). The SCP concept was introduced already during the First World War primarily as a human food (Lindberg *et al.*, 2016). However, the higher production costs of SCP linked to challenges in efficient and economical cell recovery in relation

to more conventional foods and feeds is perhaps the main reason why SCP has not reached widespread commercial use so far. Established processes include the use of yeasts *Candida lipolytica* and *Candida tropicalis* with alkanes as substrate (product called Toprina), bacterium *Methylophilus methylophilus* with methane as substrate, bacterium *Pseudomonas methylotrophus* (Pruteen) with methanol as substrate, filamentous fungus *Peacilomyces variotii* grown on sulphite spent liquor of forest industry sidestream (Pekilo) and yeast *Kluyveromyces marxianus* grown on whey (Nasseri *et al.*, 2011). The reasons why the SCP concept could become more common and economically viable in future are the rising ecoawareness and the need to intensify nutrient and resource utilisation combined with the sharp price rises caused by the prospect of protein scarcity (Lindberg *et al.*, 2016).

Microalgae

Microalgae are a diverse group of unicellular or simple multicellular microorganisms with widely varying nutritive composition (Table 1). As animal feed, microalgae have several potential uses. Species high in lipids, such as 22:6n-3-enriched *Schizochytrium* sp., can be used to modify ovine (Bichi *et al.*, 2013) or bovine (Boeckert *et al.*, 2008) milk fat healthier for humans in terms of increased *trans*-11 18:1, *cis*-9, *trans*-11 18:2 and n-3 content. Algal 22:6n-3 supplementation has increased also the n-3 content of ruminant meat (Meale *et al.*, 2014), but no effects were found on methane production (Moate *et al.*, 2013). In turn, microalgae or defatted microalgae residues high in CP (e.g. *Spirulina platensis* and *Chlorella vulgaris*), or high in carbohydrates can substitute conventional protein (Lamminen *et al.*, 2017) or energy feeds (van Emon *et al.*, 2015), respectively.

The AA composition of microalgae generally compares favourably to soya bean meal (Becker, 2013) and rapeseed meal (Feedipedia, 2018; Luke, 2018), but may vary significantly between species (Table 1). However, in comparison to rapeseed meal and soya bean meal, microalgae protein is often lower in histidine, which is typically the first AA limiting milk production on grass silage and cereal-based diets (e.g. Vanhatalo *et al.*, 1999). The protein degradability of many microalgae species is suggested to be higher than that of rapeseed (Costa *et al.*, 2016; Lamminen *et al.*, 2017), soya bean and cottonseed meals (Costa *et al.*, 2016), but this can possibly be affected by the growing and harvesting conditions of microalgae (Lodge-Ivey *et al.*, 2014). Compared to the conventional protein or energy feeds, large doses of microalgae or defatted microalgae residue may impact negatively on feed intake of ruminants depending on microalgae composition (van Emon *et al.*, 2015; Costa *et al.*, 2016; Lamminen *et al.*, 2016 and 2017). The palatability of microalgae can possibly be improved by feed processing, for example, pelleting (Hintz *et al.*, 1966). Compared to rapeseed meal, microalgae have not affected milk yield, but decreased the milk protein yield of dairy cows in late lactation, which together with decreasing N utilisation for milk production suggests that the protein value of microalgae is possibly slightly lower than that of rapeseed meal

(Lamminen *et al.*, 2017), but similar to soya bean protein (Table 3).

The local on-farm production of microalgae in ponds or in closed photoreactors connected to animal drinking water system could lower the energy inputs of feed drying, preservation and transportation making microalgae cultivation in future a viable concept also in the extensive farming. Indeed, microalgae have successively been distributed through drinking water (Panjaitan *et al.*, 2010) to growing cattle grazing low quality grasses to improve microbial protein production in the rumen and diet digestibility (Panjaitan *et al.*, 2015). In addition, microalgal-derived renewable biofuels have high potential to replace fossil fuels of diminishing reserves in future. The cost for the biofuels production from microalgae is not yet competitive with fossil fuels, but with advancing technologies and possible government incentives it may soon become profitable (Milano *et al.*, 2016) thus providing defatted microalgae residues for livestock in a mass-scale.

Seaweeds

Seaweeds are complex multicellular organisms growing in salt water or a littoral zone of marine environment (van der Spiegel *et al.*, 2013). They can be of many different shapes, sizes, colours and composition. Fresh seaweed contains very large amounts of water (700 to 900 g/kg DM) and needs to be consumed quickly or preserved by, for example, drying or ensiling. Brown algae (*Phaeophyceae*) are of lesser nutritional value than red (*Rhodophyceae*) and green algae (*Chlorophyceae*) due to lower CP content (up to 140 v. up to 500 and 300 g/kg DM, respectively). The protein content of marine seaweeds varies between seasons, but *in situ* rumen degradable protein remains unaffected with high inherent variability between algal species (24% to 51% of CP; Tayyab *et al.*, 2016). Protein in all seaweeds is typically deficient in essential AA except for methionine (Makkar *et al.*, 2016; Table 1).

Seaweeds are low in cellulose (about 40 g/kg DM) but rich in specific complex carbohydrates (e.g. alginate, laminarin and fucoidan). Step-wise increase in the levels of seaweeds in the diet may enable rumen microbes to adapt and utilise these compounds (Makkar *et al.*, 2016). Seaweeds concentrate heavy metals and minerals from seawater and contain several times the ash content of land plants that limits their gross energy value and requires regular monitoring (van der Spiegel *et al.*, 2013; Makkar *et al.*, 2016).

Makkar *et al.* (2016) have recently reviewed in detail the nutritive value of seaweed indicating that some species have the potential to contribute to the protein and energy needs of ruminants (e.g. *Macrocystis pyrifera*, *Palmaria palmata*, *Laminaria digitata*, *Ulva lactuca*), while others contain a number of bioactive compounds, which could be used as prebiotics for enhancing production and health status of animals (e.g. *Ascophyllum nodosum*). Moreover, some seaweed species have shown potential to mitigate ruminal methane production *in vitro* depending on the basal diet (Maia *et al.*, 2016). The seaweeds used for animal feeding

can be cultivated or harvested in the wild (Table 4; Makkar *et al.*, 2016; Tayyab *et al.*, 2016) serving to mitigate nutrient loading and to counteract eutrophication processes (Lindberg *et al.*, 2016). However, high collection rates in the wild have impaired the equilibrium of coastal ecosystems (Makkar *et al.*, 2016). In addition, increased cultivation of seaweeds may promote increased production of bromoform, a metabolic by-product of seaweeds that causes the depletion of atmospheric ozone layer (Carpenter and Liss, 2000).

Duckweeds

Duckweeds are monocotyledonous, small floating plants with no stems or true leaves of the botanical family *Lemnaceae* comprising of four genera (*Lemna*, *Spirodela*, *Wolffia* and *Wolffiella*). Duckweeds are found worldwide, but they grow best in stagnant water between 17.5°C and 30°C (Heuzé and Tran, 2015a) and may have a 50% biomass increase every two days (van Krimpen *et al.*, 2013). Thus, duckweed is a potential novel nutrient source for herbivores worldwide. Only few studies have been performed on duckweed in ruminants (van der Spiegel *et al.*, 2013). Overall, duckweed is consumed well in both dried and fresh forms (Heuzé and Tran, 2015a) and it can supply a significant proportion of protein and other nutrients to animals with no significant adverse effects on performance (Cheng and Stomp, 2009; Zetina-Cordoba *et al.*, 2013).

The duckweed protein is much lower in essential AA histidine, methionine and lysine compared to that of soya bean and rapeseed expeller (Table 1) that may limit duckweed's production responses relative to them. Estimates of ruminal protein degradability vary widely between 50% and 80% (Heuzé and Tran, 2015a). Duckweed contains significant amounts of ash and NDF (Table 1), but has low-lignin content (57 g/kg DM; Heuzé and Tran, 2015a). It has therefore potential to substitute also forage (Zetina-Cordoba *et al.*, 2013) and minerals (particularly P; van der Spiegel *et al.*, 2013) in ruminant diets. Nevertheless, high oxalic acid content may restrict the use of duckweed for livestock (van der Spiegel *et al.*, 2013).

Similarly to microalgae, local on-farm production of duckweed, for example, in ponds may offer a viable concept for ruminant feed production in future. Nutrient scavenging from field runoffs, manure and greywater by duckweeds has potential to reinforce circular economy practices at farm level and to decrease the environmental footprint of ruminant-based food production systems. The very high growth rate (van Krimpen *et al.*, 2013) enables that duckweed could be regularly harvested and fed to animals as fresh. Feeding fresh duckweed also limits the costs related to drying and preservation on-farm. Due to much bigger particle size relative to microalgae, simple mechanical harvesting of duckweed is feasible.

Conclusions

In the short term, the seeds and whole crop forages of N-fixing grain legumes as well as by-products from food and

biofuel industries have the greatest potential to replace or supplement traditional crops in ruminant rations in the intensive and extensive production systems in the temperate zones (summarising Figure 1). Lipid-rich camelina expeller, as an example, beneficially modifies the fatty acid composition of ruminant products with potential to mitigate simultaneously enteric methane formation, whereas the oil fraction of seeds could be used as an on-farm biofuel to increase the energy independence of farmers. In the tropics, the leaves of fodder trees and shrubs (e.g. cassava, *Leucaena* sp., *Flemingia* sp.) are good protein supplements for ruminants especially in the extensive production systems where the potential to improve diet digestibility and to mitigate enteric methane emissions is the highest. Combined food-feed production system to improve animal productivity and the efficiency of nutrient recycling as well as to decrease footprint on environment is recommended to smallholders (summarising Supplementary Figure S1), whereas detoxified jatropha meals could be suited for larger-scale feed and animal production in the tropics.

In the long term, microalgae and duckweed of high-yield potentials may become economically competitive local protein and fibre sources, respectively, for ruminants worldwide (Figure 1). This is due to the independence of their production from arable land and weather conditions while animal performance and product quality remain comparable to the traditional feeds. Microalgal derived renewable biofuels have a high potential to replace fossil fuels of diminishing reserves in future, thus providing defatted microalgae residues for intensive livestock farming in a mass-scale. Furthermore, on-farm production of microalgae connected to animal drinking water system could lower energy inputs of feed drying, preservation and transportation making microalgae competitive feed ingredient also in extensive farming. Exploitation of vast nutrient reserves in forests both in the temperate and tropical zones warrants further research on their feed value, the breaking of lignin-linkages of wood material and subsequent animal production responses.

Under the climatic conditions changing at an accelerating pace, the ruminant-based livestock systems in both temperate and tropical environments are very flexible in the types of biomasses that can be used as feeds. Despite the environmental footprint of ruminants, their importance in food production system cannot be ignored because of their unique ability to naturally consume fibrous vegetable material not exploitable to humans and other monogastrics and convert it to milk and meat of high nutritive value. Transition to ruminant diets comprising fibrous feed sources supplemented exclusively on alternative and novel feeds has great potential to improve sustainability of ruminant-derived food production, which will not compete with human-edible food materials.

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Supplementary material

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