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Effects of different lactic acid bacteria groups and fibrolytic enzymes as additives on silage quality: A meta-analysis

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ABSTRACT

A database was developed from 97 articles and was used to examine the effect of inoculant rate of obligate homofermentative and facultative heterofermentative lactic acid bacteria (OF-LAB) and obligate heterofermentative LAB (O-LAB) on silage quality using meta-analysis. This study also compared LAB inoculant groups with or without fibrolytic enzyme on the quality of legumes and forages based-silage. Results from regression equations showed that elevating levels of OF-LAB linearly reduced pH and increased lactic acid (LA) during ensiling but had no effect on aerobic stability. Conversely, O-LAB linearly increased aerobic stability. Compared to control group, LAB containing fibrolytic enzymes decreased pH by 12.15% and increased LA and neutral detergent fibre (NDF) by 58.94% and 12.23% respectively which is the highest than other inoculant groups. In conclusion, although all types of inoculants are effective to improve silage quality, response of plant materials to inoculants containing fibrolytic enzymes varied.

1. Introduction

Silage inoculants are among the most extensively studied technology in ruminant feed preservation over decades. Up to now, there has been continuous effort in searching the most effective inoculant to reach better efficiency of ensiling. Lactic acid bacteria (LAB) have long been utilized as silage inoculants due to their effectiveness in conserving nutritional value of forage biomass as well as to inhibit pathogenic growth and spoilage (Wang et al., 2019c; Weinberg and Muck, 1996). There are three commonly LAB inoculants according to their fermentative products and benefits: obligate homofermentative, facultative heterofermentative, and obligate heterofermentative LAB (Bernardi et al., 2019). The first and second groups are beneficial to maintain nutrients loss because they can rapidly reduce pH as well as deleterious microbes by producing lactic acid (LA) from the conversion of soluble carbohydrates. On the other hand, obligate heterofermentative LAB not only produce LA but also organic acid (i.e. acetic acid, formic acid), carbon dioxide, and ethanol which are effective as antifungal and to prolong the aerobic stability (Oliveira et al., 2017; Wang et al., 2020). In the commercial products, they may contain only single strain of LAB (Yang et al., 2019) or a mixture of more than two types of LAB (Amado et al., 2012; Zielińska and Fabiszewska, 2018).

More recently, driving efforts to explore the potential use of enzymes as part of pretreatment technology in silage have become an attractive

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innovation to optimize nutrient digestibility as well as for other purpose such as to produce single cell protein for feedstock (Z. Dong et al., 2020b; Machado et al., 2020; Pihlajaniemi et al., 2020). In ensiling, a number of fibrolytic enzymes such as cellulase, β-glucanase, and xylanase or yeast producing enzymes such as *Aspergillus niger*, *Saccharomyces cerevisiae*, and *Trichoderma viride cellulose* have been incorporated in the inoculants (Li et al., 2018; Queiroz et al., 2012a). They are expected to breakdown the cell wall carbohydrate thus provide more fermentable substrate (i.e. glucose) for the growth of LAB. Theoretically, the ability of enzymes to release more substrate for LAB growth could stimulate higher LA production thus improve fermentation quality of the silage. However, there were some inconsistent results among experiments. While some reports showed an improvement effects on silage quality and digestibility, no beneficial effects were also occurred when employing fibrolytic enzymes combined with LAB inoculants (Keles and Demirci, 2011; Lynch et al., 2015; Zhang et al., 2020). These discrepancies may be attributed to the plant materials used since their nutritional contents varied. Thus, quantifying the effect of incorporating enzymes on specific type of plants is important.

To date, hundreds of articles have discussed the effect of inoculants on silage quality. In line with the increasing evidences, some meta-analysis studies were carried out (Bernardi et al., 2019; Blajman et al., 2020; Kleinschmit and Kung, 2006; Oliveira et al., 2017; Rabelo et al., 2019). Although those studies have well-summarized the inoculant's effects quantitatively, however, all of the authors did not consider the presence of enzyme as a factor. Thus, there may a shortage of enzyme effects. Our study, therefore aimed to fill the shortage of knowledge to better understand the efficacy of enzyme when incorporating together with LAB based inoculants. In addition, we also quantified the effect of fibrolytic enzymes incorporated to the LAB inoculants on different type of plant materials silage.

2. Materials and methods

2.1. Literature search and selection criteria

A literature search was conducted using the online scientific platforms of Google Scholar, Science Direct and PubMed Central to search for studies of the utilizing of inoculants in silage operations. The keywords 'silage', 'microbial inoculant', 'lactobacillus', 'yeast' and 'enzyme' were used in the screening process of articles. To be eligible for inclusion in the present meta-analysis, papers were strictly selected following the protocol of Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) as a systematic and reproducible method. Accordingly, studies were selected based on the following inclusion criteria: (a) published in English; (b) contained control group which did not use inoculant (control) and treatment groups using inoculants; (c) reported the forage or crops used and the type or strain of LAB/yeast, as well as their inoculation rates; (d) ensiling was conducted for at least 30 days; and (e) reported replication and variance (standard deviation, SD or standard error or means, SEM).

A flowchart explaining the process of study selection based on PRISMA protocol is provided in Fig. 1. Briefly, a total of 526 peer-reviewed research articles were identified based on the title of the papers. According to the criteria aforementioned, 169 articles were selected while 357 articles were excluded. After carefully reviewing the full texts, contents and variables, we also excluded a further 69 studies for the following reasons: (i) the variable did not meet the minimum criteria (41); (ii) another additive such as organic acid, molasses or salt was used (11); (iii) incomplete information on the method and unspecific LAB and level was provided (8); (iv) did not use controls (6); and (v) not published in a peer-reviewed journal (3). Finally, 97 articles comprising 155 experiments with 606 treatment means were integrated in the database and used for the meta-analysis.

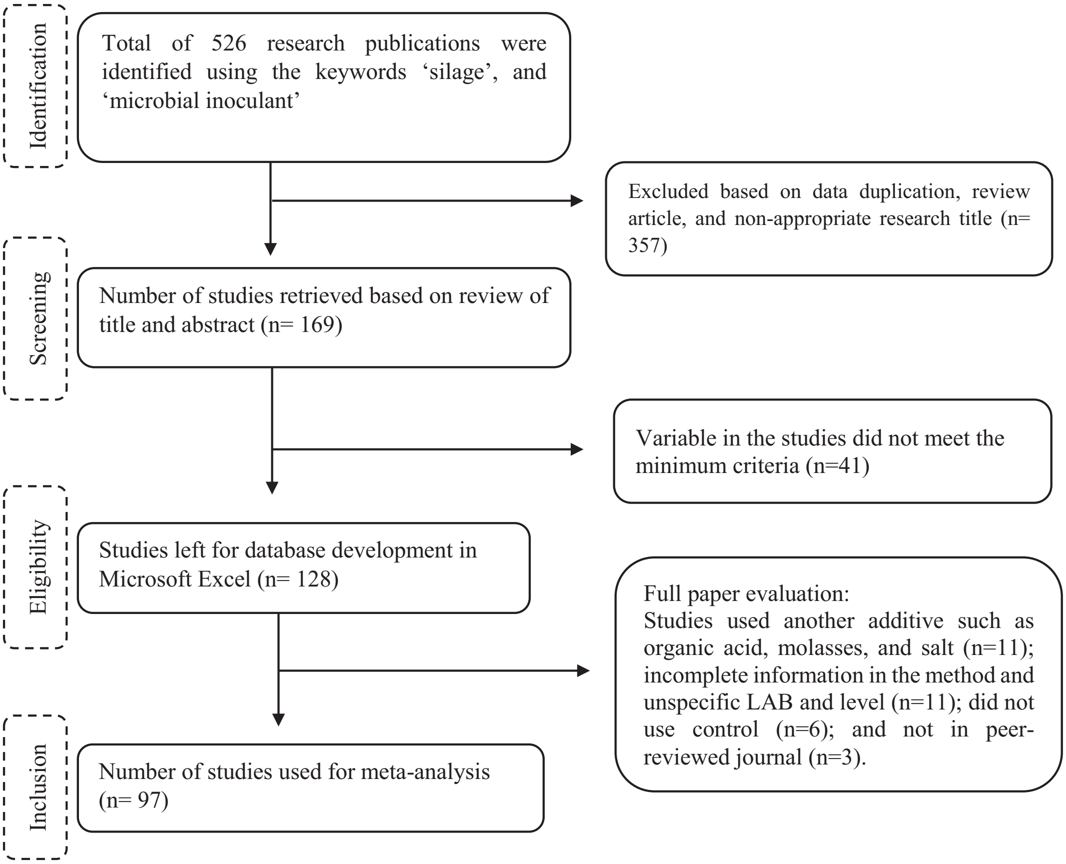


Fig. 1. Flow charts of publications utilized for the meta-analysis.

2.2. Database development

Information on authors, number of replications, study design, ensiling period, source of variability and response variables were entered in a Microsoft Excel spreadsheet. Sources of heterogeneity included in the dataset were plant materials used, type of silo, type of inoculant, and inoculation rate. Response variables included in the database were chemical composition before and after ensiling [DM; crude protein (CP); neutral detergent fibre (NDF); acid detergent fibre (ADF); water soluble carbohydrate (WSC)], fermentation profile [pH; ammonia (NH_3); lactic acid; acetic acid (AA); propionic acid (PA); butyric acid (BA); and ethanol], nutrient digestibility (DM, CP, NDF and ADF), and microbial composition (LAB, yeast, and mould). All data of the response variables were converted into the same unit of measurement to allow the calculations and analyses.

2.3. Statistical analysis

The meta-analysis was performed using mixed model analysis considering the inoculants as fixed effects and the different studies as random effects (St-Pierre, 2001). The analysis was conducted following the PROC MIXED procedure of SAS (SAS Studio 3.8, University Edition, 2018) to regress the effect of inoculation rates (given as log CFU/g fresh matter) on silage quality. As indicated in Table 1, there were large number of bacterial strains used for ensiling. Thus, we distinguished the type of inoculant as a group of obligate homofermentative or facultative heterofermentative LAB (OF-LAB) and obligate heterofermentative LAB (O-LAB), reflecting the different mode of actions in their fermentation process. Inoculation rate of each group was treated as continuous predictor where the effect was assessed using the following mixed model:

$$Y_{ij} = B_0 + B_1 X_{ij} + B_2 X_{ij}^2 + s_i + b_i X_{ij} + e_{ij}$$

where Y_{ij} = the expected output for predictor variable Y at level j from the variable X as a continuous predictor variable in the study i; B_0 = intercept across experiments (fixed effect); B_1 = linear model coefficient of Y on X (fixed effect); B_2 = quadratic model coefficient of Y on X (fixed effect); X_{ij} = value of the continuous predictor variable X (inoculation rate); s_i = random effect of experiment i; b_i = random effect of experiment i on the model coefficient of Y on X in experiment i; and eij = the residual error. The 'study' was declared as the CLASS statement. Number of replicates was used for weighting the data using a WEIGHT statement while an unstructured variance–covariance matrix (type = UN) was declared in the random effects part of the model. This was used to avoid positive correlation between intercepts and slopes (St-Pierre, 2001). Statistical models used for the continuous variable were p-values for intercepts and slopes, Akaike's information criterion, and root mean square error (RMSE) (Jayanegara et al., 2014).

In addition, as we recognized that microbial strains used as inoculant may differently affect silage quality, we classified the type of LAB as discrete predictors into four categories: (1) single strain of homolactic or facultative heterolactic LAB [**hos-LAB** referred to *Lactobacillus plantarum*, *L. acidophilus*, *L. curvatus*, *L. casei*, *L. fermentum*, *L. reuteri*, *L. salivarius*, *Pediococcus pentosaceus*, *P. acidilactic*, *P. cerevisiae*, *Enterococcus faecium*, etc.]; (2) single strain of obligate heterolactic LAB (**hes-LAB** referred to *L. farraginis*, *L. hilgardii*, *L. brevis* and *L. buchneri*); (3) multiple strains of hos-LAB which contained more than one hos-LAB (hom-**LAB**); (4) and multiple strains which containing hos-LAB and hes-LAB (**MS-LAB**). Additionally, as we also considered the enzymes as predictor variables, two additional groups of enzyme treatments (**EN**) and combinations of enzymes and LAB (**MSE**) were included. In total, there were seven categorical treatments including the control. Furthermore, these discrete variables were examined two types of plant material used in the silage making in which either forage and crops as they have low-to-moderate CP content (corn, sorghum, barley, Bermuda grass, Italian ryegrass, Napier grass, *Digitaria eriantha*, Guinea grass, oat crop, rice straw and sugarcane) or legumes and high CP plants (alfalfa, mulberry and moringa leaves) by using the following mathematical model:

$$Y_{ij} = \mu + S_i + \tau_j + S\tau_{ij} + e_{ij}$$

where Y_{ij} = the predicted output for predictor variable Y; μ = overall mean of the treatment; S_i = random effect of i study; τ_j = fixed effect of the j level; $S\tau_{ij}$ = random effect between i study and the j level; and eij = residual error. A significant effect was declared at $p \leq 0.05$, and a tendency to be significant was considered when $0.05 < p \leq 0.10$. Tukey's HSD test was performed to compare least-square means among the experimental groups. Additionally, the relationships among response variables were visualized by the heatmap.2 feature from the *gplots* package in the R Console Version 3.6.1 (R Core Team, 2019) and are provided in Figs. 2 and 3. The Spearman correlations among response variables presented in Figs. 4 and 5 were visualized by the heatmap colour function in Microsoft Excel.

3. Results

3.1. Description of the database included in the meta-analysis

In this present meta-analysis, we compared 606 treatment means consisting of 451 inoculated groups and 155 control groups. The studies included are presented in Table 1 and the descriptive statistics are provided in Table 2. Our database showed large variations, as can be seen from the standards of deviation across the variable outcomes. This is common in meta-analyses since there is a broad representation of materials used in the studies included, especially in regard to types of substrate and inoculants. Of the total inoculants used, 44.4% corresponded to the homolactic or facultative heterolactic group, 32.3% belonged to the obligate heterolactic group and the rest were multiple strains containing both OF-LAB and O-LAB. Among LAB, *L. plantarum* and *L. buchneri* were the most frequently used, accounting for 29.8% and 14.1%, respectively.

Ensiling was performed in laboratory silos (1.5 L of anaerobic glass jars and <20 L lof aboratory plastic-bag silos, 86.1%) and farm-scale silos (13.9%) for periods of 30 days to 1095 days, with inoculation rates of 1×10^4–8×10^5 (34.6%), 1×10^6–5×10^6 (37.2%), 2.1×10^7–4.5×10^9 (9.7%), and $>1 \times 10^{10}$ CFU/g of fresh matter (4.2%), respectively. In addition to the inoculants, 19.1% of the studies used fibrolytic enzymes incorporated in the commercial LAB inoculant products. All studies described substrate used (of which 61.1% were forage, 20.3% were legumes, and 18.5% were other crops). Corn forage and alfalfa dominated the plants used across studies (29.0% and 14.9%, respectively). The crops used were oats, barley, wheat, sorghum, rice straw, sugarcane and soyabean.

3.2. Regression analysis of the relationship between LAB inoculation rate and silage quality

Regression equation models of the relationship between OF-LAB and O-LAB inoculation rates and silage quality are provided in Tables 3 and 4, respectively. The results revealed that the chemical composition of silage was not influenced by levels of either OF-LAB or O-LAB. A linear decrease in pH and a quadratic decrease in NH_3 were observed in increasing rates of OF-LAB ($P < 0.05$), but these parameters were not influenced by O-LAB level. Fermentative parameters of LA, AA, LAA/AA and BA were not affected by increasing level of OF-LAB, whereas PA decreased linearly ($P < 0.05$). Addition of O-LAB increased both AA and PA linearly ($P < 0.05$), but had no effects on LA and BA. Ethanol production reduced linearly with OF-LAB inoculation ($P < 0.001$). Conversely, that figure increased with O-LAB inoculation following a curvilinear pattern ($P < 0.001$).

Inoculation rate either for OF-LAB or O-LAB had no effects on

Table 1
Studies included in the meta-analysis.

Reference	Study	Exp	Substrate	Type of silo	Ensiling period (d)	LAB type*	Enzyme type**	Inoculant rate (log CFU/g FM)
(Kung et al., 1991)	1	1	Wilted alfalfa	Lab	56	1		0–5.00
(Meeske et al., 1993)	2	2	Sorghum forage	Lab	31	1, 13, 15, 30	a, c, d	0–6.00
(Stokes and Chen, 1994)	3	3	Corn	Lab	56	1, 13		0–5.04
(Sheperd and Kung, 1996)	4	4	Corn	Lab	196		a	
(Kreikemeier and Bolsen, 1997)	5	5–6	Corn forage	Farm-scale	270	1, 11		0–9.00
(McAllister et al., 1998)	7	7	Alfalfa	Farm-scale	84	1, 12		0–6.00
(Higginbotham et al., 1998)	8	8	Corn silage	Lab	90	1, 15, 17		0–10.48
(Meeske and Basson, 1998)	9	9	Maize silage	Lab	95	1, 9, 10	a, c	0–6.00
(Cai et al., 1998)	10	10–14	Alfalfa	Lab	30	1, 8, 30		0–5.00
(Meeske et al., 1999)	12	15	*Digitaria eriantha*	Farm-scale	44	1, 13, 15	a, c, d	0–6.00
(Filya et al., 2000)	13	16	Fresh wheat crop	Lab	65	1, 5, 12		0–6.18
(Whiter and Kung, 2001)	14	17–18	Alfalfa	Lab	45	1		0–5.00
(Meeske et al., 2002)	15	19	Whole crop oats	Farm-scale	270	1, 13, 15	c, d, f	0–7.32
(Taylor and Kung, 2002)	16	20	Corn	Lab	166	1, 2		0–10.7
(Filya, 2003)	17	21–22	Corn and sorghum	Lab	90	1, 2		0–6.00
(Adesogan et al., 2003)	18	23	Wheat	Lab	68	2, 7, 25		0–5.00
(Adesogan et al., 2004)	19	24	Bermudagrass	Lab	60	2, 11	c, f, h	0–9.00
(Nishino et al., 2004)	20	25–26	Corn	Lab	60	2, 8		0–6.00
(Weinberg et al., 2007)	21	27–28	Wheat and corn forage	Lab	60	1, 2, 5, 11, 12		0–6.00
(Filya et al., 2006)	22	29–30	Alfalfa	Lab	30	1, 5, 12, 15, 17		0–6.00
(Hu et al., 2009)	23	31–31	Corn forage	Farm-scale	240	1, 2		0–12.6
(Nkosi et al., 2009)	24	33–34	Corn forage	Lab & Farm scale	60	1, 2, 11		0–5.48
(Huisden et al., 2009)	25	35	Corn forage	Lab	135	2, 11, 12	f, g, h	0–11.2
(Kang et al., 2009)	26	36–37	Corn forage	Lab	110	2, 8		0–9.00
(Lima et al., 2010)	27	38–41	Soybean and sorghum	Lab	30	1		0–5.48
(Nkosi and Meeske, 2010)	28	42–43	TMR with potato hash	Lab & Farm-scale	90	2		0–6.48
(Schmidt and Kung, 2010)	29	44–48	Corn	Lab	120	2, 11		0–10.6
(Keles and Demirci, 2011)	30	49	Triticale–Hungarian vetch herbage	Farm-scale	90	1, 11, 12, 14	a, c, d, e	0–6.00
(Arriola et al., 2011)	31	50	Corn forage	Farm-scale	363	11, 24	c	0–5.00
(Bayatkouhsar et al., 2011)	32	51	Corn forage	Farm-scale		1, 2, 8, 10, 30		0–6.00
(Tabacco et al., 2011)	33	52–53	Corn forage	Farm-scale	240	2, 8		0–9.00
(Bureenok et al., 2011)	34	54	Ruzigrass (*B. ruziziensis*)	Lab	45	30		0–5.64
(Queiroz et al., 2012a)	35	55–56	Corn forage	Farm-scale	166	2, 11		0–5.70
(Mohammadzadeh et al., 2012)	36	57	Corn forage	Farm-scale	120	1, 2, 8, 11, 12		0–5.18
(Acosta Aragón et al., 2012)	37	58	Corn forage	Farm-scale		1, 3, 12		0–5.00
(Amado et al., 2012)	38	59–60	Corn and ryegrass	Lab	30	1, 2, 12, 13, 21		0–8.00
(Queiroz et al., 2012b)	39	61–63	Corn forage	Lab	97	2, 11, 27	f, h, j	0–9.00
(Queiroz et al., 2013)	40	64	Corn forage	Farm-scale	120	1, 11, 12, 21, 27		0–6.00
(Diaz et al., 2013)	41	65	Corn forage	Lab	225	2, 11, 27		0–5.00
(Ferreira et al., 2013)	42	66	Elephant grass	Lab	60	12, 24		0–6.00
(Thomas et al., 2013)	43	67–70	Sorghum crop	Lab	120	1, 2, 12, 13	f, h	0–5.00
(Santos et al., 2013)	44	71	Corn	Lab	48	1, 2		0–6.00
(Ávila et al., 2014)	45	72	Sugar cane	Lab	61	1, 3, 4		0–9.00
(Lynch et al., 2014)	46	73	Alfalfa	lab	70	2, 11, 12	a, b	0–5.60
(Amanullah et al., 2014)	47	74	Barley	Lab	100	1		0–5.18
(Comino et al., 2014)	48	75–78	Corn forage (harvest stage 1)	Lab	260	2, 8		0–9.00
(Addah et al., 2014)	49	79–82	Whole crop barley	Lab and farm-scale	64	1, 2, 8		0–5.45
(Yuan et al., 2015)	50	83	TMR	Lab	45	1		0–6.00
(Nkosi et al., 2015)	51	84	Potato has + wheat bran	Farm-scale	90	1, 2, 12	d, m	0–5.78
(Jin et al., 2015)	52	85	Barley	Lab	90	1, 2, 8, 12	b, h	0–8.00
(Lynch et al., 2015)	53	86–87	Corn	Lab	70	1, 2, 8	b, h	0–5.11
(Li et al., 2016b)	54	88	Rice straw	Lab	60	1, 2, 8		0–6.00
(Nkosi et al., 2016)	55	89–90	Soybean forage	Farm-scale	90	30		0–5.54
(Liu et al., 2016)	56	91	TMR, alfalfa based	Lab	60	1	a, c	0–6.00
(Li et al., 2016a)	57	92	Rice straw	Lab	60	1, 2, 8		0–6.00
(Ellis et al., 2016)	58	93	Ryegrass	Lab	21	30		0–5.00
(Khota et al., 2016)	59	94–97	Guinea and Napier grass	Lab	30	1, 8	a, i	0–5.00
(Ogunade et al., 2017)	60	98	Corn forage	Lab	120	1, 2		0–6.00
(Romero et al., 2017)	61	99–100	Oat crop	Lab	217	2, 11		0–12.6
(Abdul Rahman et al., 2017)	62	101	Whole corn	Lab	1, 31	1, 24		0–5.00
(Daniel et al., 2018)	63	102	Corn	Lab	186	1, 12, 21		0–5.18
(Liu et al., 2018)	64	103	Alfalfa	Lab	65	1, 2		0–6.00

(continued on next page)

Table 1 (*continued*)

Reference	Study	Exp	Substrate	Type of silo	Ensiling period (d)	LAB type[*]	Enzyme type[**]	Inoculant rate (log CFU/g FM)
(Zielińska and Fabiszewska, 2018)	65	104–105	Corn	Lab & farm-scale	48	1, 2, 6, 7		0–6.00
(Khota et al., 2018)	66	106–109	Guinea and Napier grass	Lab	30		a	0–6.00
(Lara et al., 2018b)	67	110	Corn forage	Farm-scale	170	1, 21		0–10.00
(Li et al., 2018)	68	111	Alfalfa	Lab	60	1	a	0–6.00
(Joo et al., 2018)	69	112	Rye grass	Lab	100	1, 2		0–5.18
(Gallo et al., 2018)	70	113–114	Corn forage	Lab	32	2, 21		0–5.40
(Basso et al., 2018)	71	115	Maize	Farm-scale	70	2		0–5.00
(Guo et al., 2018)	72	116	Wilted alfalfa	Lab	90	1, 2		0–6.00
(Zhao et al., 2018)	73	117–118	Oat crop	Lab	60	1, 12, 13	*l*	0–9.40
(Yang et al., 2019)	74	119–120	Alfalfa	Lab	30	1		0–6.00
(Xu et al., 2019b)	75	121	Corn forage	Lab	118	2	k	0–9.00
(Zhang et al., 2019)	76	122	Corn forage	Farm-scale	45	1, 2, 8, 12		0–29.0
(Restelatto et al., 2019)	77	123	TMR	Lab	60	1, 2		0–5.00
(Wang et al., 2019a)	78	124–125	Mulberry leaf	Lab	60	8		0–6.00
(Liu et al., 2019)	79	126	Barley crop	Lab	60	1, 2, 8		0–5.00
(Wang et al., 2019b)	80	127–128	Moringa leaves	Lab	60	1, 21		0–5.00
(Zhao et al., 2019)	81	129	Rice straw	Lab	60	1		0–6.00
(da Silva et al., 2019)	82	130–131	Corn	Lab	300	2		0–5.00
(Li et al., 2019)	83	132–136	Ryegrass	Lab	60	1, 2		0–6.00
(Wang et al., 2019b)	84	137–138	Moringa leaves	Lab	60	15, 21		0–5.00
(Su et al., 2019)	85	139–140	Alfalfa	Lab	60	7	a	0–6.00
(Zhang et al., 2019)	86	141	Corn forage	Farm-scale	45	1, 2, 8, 12		0–29.0
(Nascimento Agarussi et al., 2019)	87	142	Alfalfa	Lab	56	1, 3, 5, 11, 14		0–5.00
(Zhou et al., 2019)	88	143	Corn	Lab	90	1	k	0–5.48
(Zhang et al., 2020)	89	144–146	Mulberry	Lab	30	1	a	0–6.00
(Chen et al., 2020)	90	147	Alfalfa	Lab	90	1		0–5.00
(Z. Dong et al., 2020a)	91	148	Napier grass	Lab	30	30	k	0–31.16
(Liu et al., 2020)	92	149	Barley	Lab	60	30		0–5.00
(Guo et al., 2020)	93	150	Wilted alfalfa	Lab	60	1, 14		0–6.00
(Vidya Paradhipta et al., 2020)	94	151	Ryegrass	Lab	90	3, 15		0–5.08
(Z. Dong et al., 2020b)	95	152	Mulberry leaves	Lab	60	1		0–6.00
(Amaral et al., 2020)	96	153	Elephant grass	Lab	60	1, 2, 3, 4, 17		0–6.70
(Saylor et al., 2020)	97	154	Whole plant corn	Lab	120	1, 12, 21		0–9.00

[*] *LAB type*: 1 = *L. plantarum*; 2 = *L. buchneri*; 3 = *L. brevis*; 4 = *L. hilgardii*; 5 = *L. pentosus*; 6 = *L. reuteri*; 7 = *L. fermentum*; 8 = *L. casei*; 9 = *L. bulgaricus*; 10 = *L. acidophilus*; 11 = *Pediococcus pentosaceus*; 12 = *Enterococcus faecium*; 13 = *Pediococcus acidilactici*; 14 = *L. salivarius*; 15 = *Pediococcus cerevisiae*; 16 = *Pediococcus* spp.; 17 = *Pediococcus cerevisiae*; 18 = *Streptococcus faecium*; 19 = *Enterobacteriaceae*; 20 = *L. farciminis*; 21 = *L. lactis*; 22 = *Leuconostoc holzapfelii*; 23 = *L. farraginis*; 24 = *Streptococcus bovis*; 25 = *Leuconostoc mesenteroides*; 26 = *L. xylosus*; 27 = *Gluconobacter oxydans*; 28 = *L. farciminis*; 29 = *Leuconostoc mesenteroides*; 30 = Consortium LAB, unspecified, 31 = *Propionibacterium freudenreichii*.

[**] *Enzyme index*: a = cellulase; b = engoglucanase; c = α-amylase; d = hemmicellulase; e = pentosanase; f = β-glucanase; g = mannanase; h = xylanase; i = maicelase; j = galactomannanase; k = enzyme produced from *Saccharomyces*; l = enzyme produced from *Aspergillus niger*; m = pectinase.

digestibility of DM (DDM) and CP (DCP). However, increasing levels of OF-LAB inoculant increased NDF digestibility (DNDF) with a curvilinear pattern ($P < 0.001$). In OF-LAB inoculant, mould population increased following a quadratic pattern ($P < 0.05$) but LAB and yeast were not affected. On the other hand, LAB concentration linearly increased ($P < 0.05$) whereas yeast concentration linearly decreased ($P < 0.05$) with increasing level of O-LAB inoculation, but mould was not altered. The positive effect of O-LAB inoculation rate was observed by the increase in aerobic stability (h) with quadratic pattern ($P < 0.05$), but this was not observed in the OF-LAB inoculant.

3.3. Effect of type of inoculant on silage quality

The effects of LAB inoculants with or without fibrolytic enzymes on legume and forage silages are presented in Tables 5 and 6, while the relationship among treatments and response variables are visualized in Figs. 2 and 3, respectively. As observed on legume and forage silages, inoculants affected fermentation profile differently, in that enzyme addition failed to reduced pH on legume silage but decreased pH on forage-based silage ($P < 0.01$). In terms of fermentation quality, MSE and hom-LAB inoculants showed a greater effect in increasing LA concentration in legume-based silage ($P < 0.05$). In addition, in the legume silage, AA concentration decreased with hom-LAB treatment ($P < 0.05$) when compared to the control. As indicated in the heatmap visualization, in legume-based silage, MSE resulted in the highest increase in lactate production, in which there was a relationship with hos-LAB and MS-LAB (Fig. 3).

Similarly, hes-LAB and MSE showed a relationship with the highest increase in aerobic stability (h) in forage-based silage (Fig. 4), while the relationship between hos-LAB and hom-LAB showed significantly increased LA concentration. In forage-based silage, not only hom-LAB but also hos-LAB increased LA and concomitantly decreased AA concentrations ($P < 0.05$). In consequence with increasing the gap between LA and AA, treatment with hom-LAB had the highest LA/AA ratio in the legume silage whereas hos-LAB and hom-LAB similarly had the highest LA/AA ratio among other treatments, including the forage-based silage control ($P < 0.01$). Furthermore, a different pattern was observed for ethanol production, in which hes-LAB treatment was superior for increased ethanol concentration in legume silage while hos-LAB and hom-LAB, and enzyme when given alone (EN), showed a greater effect in increased ethanol production in forage silage compared with the control and other treatments ($P < 0.05$). When observed in legume silage, PA concentration was similar among treatments, but it was decreased significantly with hes-LAB, MSE, and EN treatments as observed in forage-based silage in comparison with the control ($P < 0.01$). Either when expressed as g/kg DM or g/total N, BA concentrations, NH_3 and WSC were not affected by the treatments in both legume-based and forage-based silage.

Additionally, we did not observe any effect of microbial inoculation on DM content, DM loss and CP content of legume- and forage-based

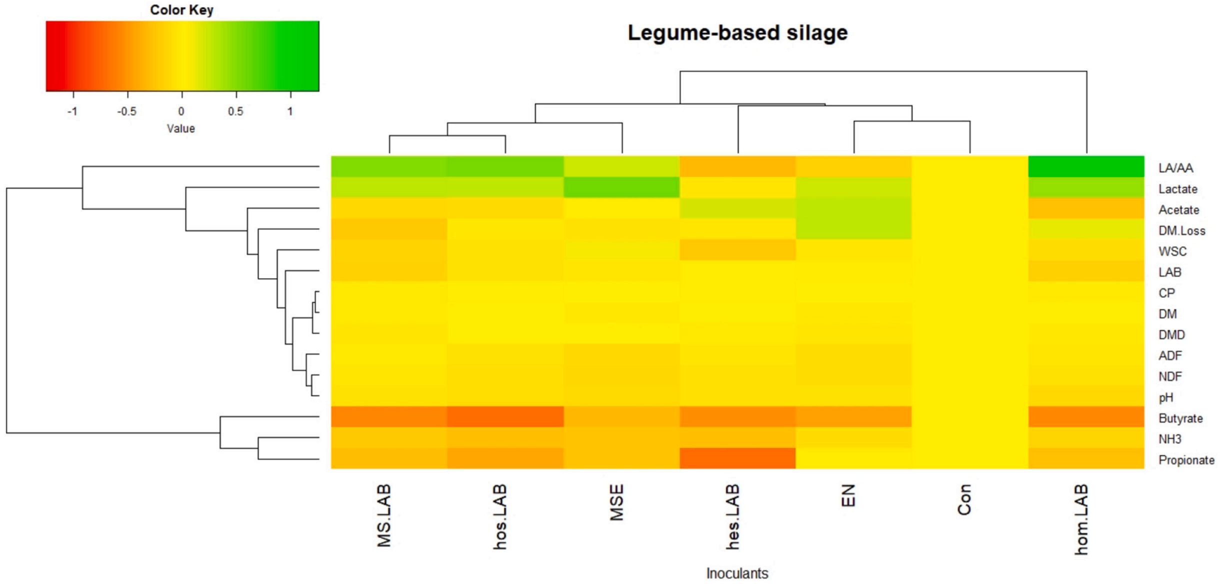


Fig. 2. Heatmap of the relationship between treatments and response variables of legume-based silage. Colors reflect trend of treatment effect from decreasing trend (red) to increasing trend (green).

DM = dry matter; CP = crude protein; WSC = water soluble carbohydrate; NDF = neutral detergent fibre; ADF = acid detergent fibre; DMD = DM digestibility; CPD = CP digestibility; NDFD = NDF digestibility; LAB = lactic acid bacteria; Con = control (without inoculant); MSE = mixed of LAB + fibrolytic enzymes; E = fibrolytic enzymes; hes-LAB = heterofermentative LAB (single strain/type); hos-LAB = homofermentative LAB (single strain/type); hom-LAB = homofermentative LAB (multiple strain/type); MS = multiple type of LAB (homofermentative + heterofermentative).

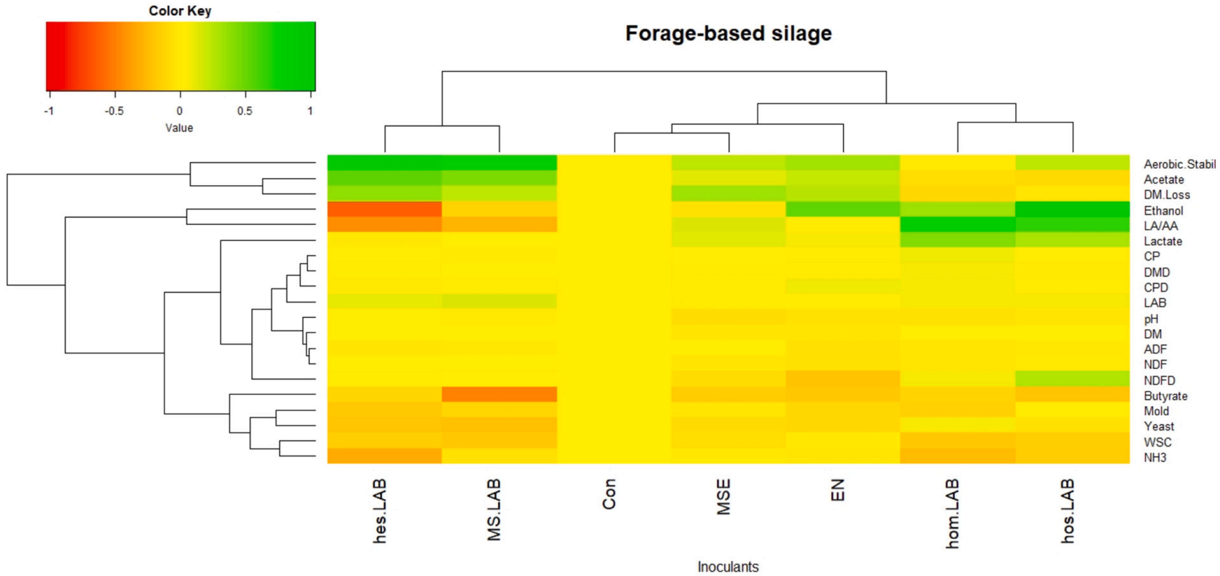
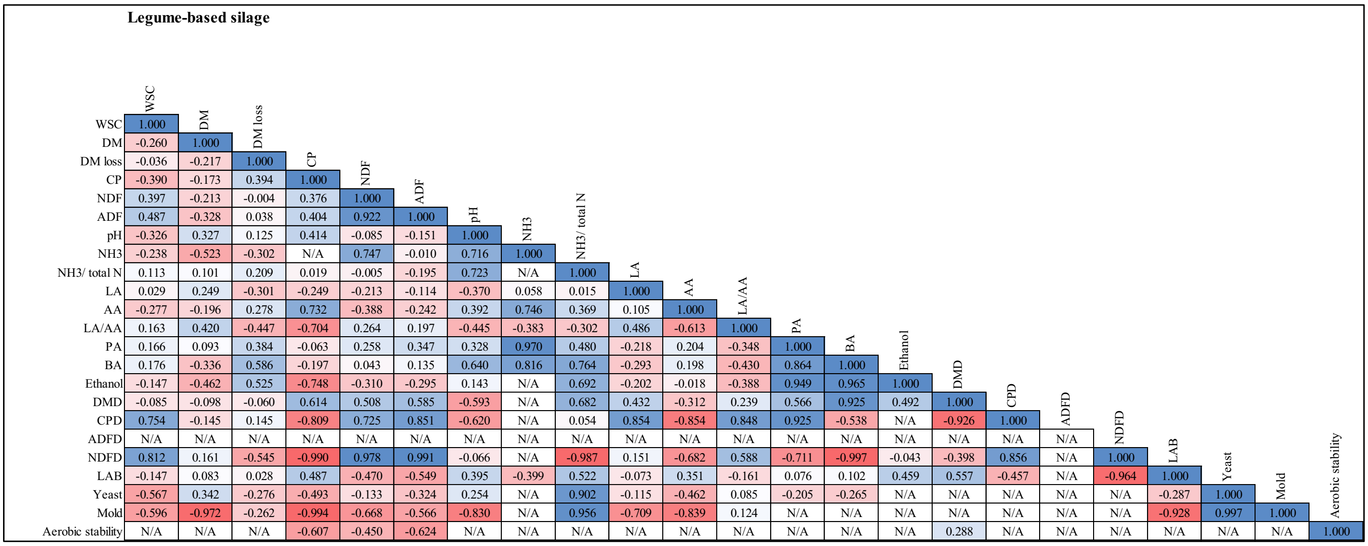


Fig. 3. Heatmap of the relationship between treatments and response variables of forage-based silage. Colors reflect trend of treatment effect from decreasing trend (red) to increasing trend (green).

DM = dry matter; CP = crude protein; WSC = water soluble carbohydrate; NDF = neutral detergent fibre; ADF = acid detergent fibre; DMD = DM digestibility; CPD = CP digestibility; NDFD = NDF digestibility; LAB = lactic acid bacteria; Con = control (without inoculant); MSE = mixed of LAB + fibrolytic enzymes; E = fibrolytic enzymes; hes-LAB = heterofermentative LAB (single strain/type); hos-LAB = homofermentative LAB (single strain/type); hom-LAB = homofermentative LAB (multiple strain/type); MS = multiple type of LAB (homofermentative + heterofermentative).

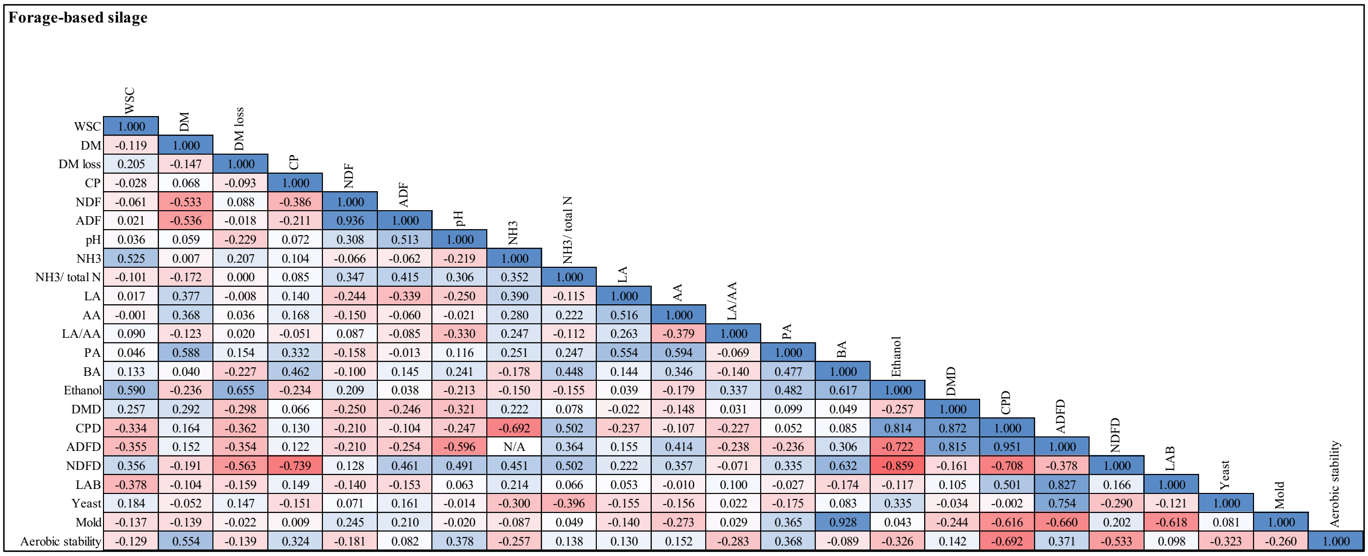
silages. Compared with the control, NDF and ADF fractions in legume silage were significantly lower in MSE, EN and hos-LAB treatments ($P < 0.01$). In forage silage, no effect was observed on NDF and ADF contents. Meanwhile, while digestibility of DM and NDF was similar among treatments in legume silage, hom-LAB and hos-LAB treatments in forage-based silage increased DMD and NDFD, respectively, when compared to the control ($P < 0.05$). With regard to microbial population, no effect was found on LAB in legume silage and mould concentration in forage silage from inoculation treatments. In forage-based silage, LAB populations in hes-LAB, hos-LAB, hom-LAB and MS-LAB treatments were observed to be significantly higher than those of the control and enzyme-associated treatments either inoculated alone (EN) or incorporated with LAB inoculant (MSE) ($P < 0.01$). Moreover, hes-LAB and MS treatments showed positive effects on the aerobic stability of forage-based silage, as these types of inoculants had longer aerobic stability (h) than the control and the other group of inoculants ($P < 0.01$).



Legume-based silage

	WSC	DM	DM loss	CP	NDF	ADF	pH	NH3	NH3/ total N	LA	AA	LA/AA	PA	BA	Ethanol	DMD	CPD	ADFD	NDFD	LAB	Yeast	Mold	Aerobic stability
WSC	1.000																						
DM	-0.260	1.000																					
DM loss	-0.036	-0.217	1.000																				
CP	-0.390	-0.173	0.394	1.000																			
NDF	0.397	-0.213	-0.004	0.376	1.000																		
ADF	0.487	-0.328	0.038	0.404	0.922	1.000																	
pH	-0.326	0.327	0.125	0.414	-0.085	-0.151	1.000																
NH3	-0.238	-0.523	-0.302	N/A	0.747	-0.010	0.716	1.000															
NH3/ total N	0.113	0.101	0.209	0.019	-0.005	-0.195	0.723	N/A	1.000														
LA	0.029	0.249	-0.301	-0.249	-0.213	-0.114	-0.370	0.058	0.015	1.000													
AA	-0.277	-0.196	0.278	0.732	-0.388	-0.242	0.392	0.746	0.369	0.105	1.000												
LA/AA	0.163	0.420	-0.447	-0.704	0.264	0.197	-0.445	-0.383	-0.302	0.486	-0.613	1.000											
PA	0.166	0.093	0.384	-0.063	0.258	0.347	0.328	0.970	0.480	-0.218	0.204	-0.348	1.000										
BA	0.176	-0.336	0.586	-0.197	0.043	0.135	0.640	0.816	0.764	-0.293	0.198	-0.430	0.864	1.000									
Ethanol	-0.147	-0.462	0.525	-0.748	-0.310	-0.295	0.143	N/A	0.692	-0.202	-0.018	-0.388	0.949	0.965	1.000								
DMD	-0.085	-0.098	-0.060	0.614	0.508	0.585	-0.593	N/A	0.682	0.432	-0.312	0.239	0.566	0.925	0.492	1.000							
CPD	0.754	-0.145	0.145	-0.809	0.725	0.851	-0.620	N/A	0.054	0.854	-0.854	0.848	0.925	-0.538	N/A	-0.926	1.000						
ADFD	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A					
NDFD	0.812	0.161	-0.545	-0.990	0.978	0.991	-0.066	N/A	-0.987	0.151	-0.682	0.588	-0.711	-0.997	-0.043	-0.398	0.856	N/A	1.000				
LAB	-0.147	0.083	0.028	0.487	-0.470	-0.549	0.395	-0.399	0.522	-0.073	0.351	-0.161	0.076	0.102	0.459	0.557	-0.457	N/A	-0.964	1.000			
Yeast	-0.567	0.342	-0.276	-0.493	-0.133	-0.324	0.254	N/A	0.902	-0.115	-0.462	0.085	-0.205	-0.265	N/A	N/A	N/A	N/A	N/A	-0.287	1.000		
Mold	-0.596	-0.972	-0.262	-0.994	-0.668	-0.566	-0.830	N/A	0.956	-0.709	-0.839	0.124	N/A	N/A	N/A	N/A	N/A	N/A	N/A	-0.928	0.997	1.000	
Aerobic stability	N/A	N/A	N/A	-0.607	-0.450	-0.624	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.288	N/A	N/A	N/A	N/A	N/A	N/A	1.000

Fig. 4. Heatmap of spearman correlation among response variables of legume-based-silage quality assessment. Colors reflect degree of correlation from low (red) to high (blue).
WSC = water soluble carbohydrate; DM = dry matter; CP = crude protein; NDF = neutral detergent fibre; ADF = acid detergent fibre; NH3, ammonia (mg/kg DM); LA, lactic acid; AA, acetic acid; PA, propionic acid; BA, butyric acid; DMD = DM digestibility; CPD = CP digestibility; NDFD = NDF digestibility; LAB = lactic acid bacteria.



Forage-based silage

	WSC	DM	DM loss	CP	NDF	ADF	pH	NH3	NH3/ total N	LA	AA	LA/AA	PA	BA	Ethanol	DMD	CPD	ADFD	NDFD	LAB	Yeast	Mold	Aerobic stability
WSC	1.000																						
DM	-0.119	1.000																					
DM loss	0.205	-0.147	1.000																				
CP	-0.028	0.068	-0.093	1.000																			
NDF	-0.061	-0.533	0.088	-0.386	1.000																		
ADF	0.021	-0.536	-0.018	-0.211	0.936	1.000																	
pH	0.036	0.059	-0.229	0.072	0.308	0.513	1.000																
NH3	0.525	0.007	0.207	0.104	-0.066	-0.062	-0.219	1.000															
NH3/ total N	-0.101	-0.172	0.000	0.085	0.347	0.415	0.306	0.352	1.000														
LA	0.017	0.377	-0.008	0.140	-0.244	-0.339	-0.250	0.390	-0.115	1.000													
AA	-0.001	0.368	0.036	0.168	-0.150	-0.060	-0.021	0.280	0.222	0.516	1.000												
LA/AA	0.090	-0.123	0.020	-0.051	0.087	-0.085	-0.330	0.247	-0.112	0.263	-0.379	1.000											
PA	0.046	0.588	0.154	0.332	-0.158	-0.013	0.116	0.251	0.247	0.554	0.594	-0.069	1.000										
BA	0.133	0.040	-0.227	0.462	-0.100	0.145	0.241	-0.178	0.448	0.144	0.346	-0.140	0.477	1.000									
Ethanol	0.590	-0.236	0.655	-0.234	0.209	0.038	-0.213	-0.150	-0.155	0.039	-0.179	0.337	0.482	0.617	1.000								
DMD	0.257	0.292	-0.298	0.066	-0.250	-0.246	-0.321	0.222	0.078	-0.022	-0.148	0.031	0.099	0.049	-0.257	1.000							
CPD	-0.334	0.164	-0.362	0.130	-0.210	-0.104	-0.247	-0.692	0.502	-0.237	-0.107	-0.227	0.052	0.085	0.814	0.872	1.000						
ADFD	-0.355	0.152	-0.354	0.122	-0.210	-0.254	-0.596	N/A	0.364	0.155	0.414	-0.238	-0.236	0.306	-0.722	0.815	0.951	1.000					
NDFD	0.356	-0.191	-0.563	-0.739	0.128	0.461	0.491	0.451	0.502	0.222	0.357	-0.071	0.335	0.632	-0.859	-0.161	-0.708	-0.378	1.000				
LAB	-0.378	-0.104	-0.159	0.149	-0.140	-0.153	0.063	0.214	0.066	0.053	-0.010	0.100	-0.027	-0.174	-0.117	0.105	0.501	0.827	0.166	1.000			
Yeast	0.184	-0.052	0.147	-0.151	0.071	0.161	-0.014	-0.300	-0.396	-0.155	-0.156	0.022	-0.175	0.083	0.335	-0.034	-0.002	0.754	-0.290	-0.121	1.000		
Mold	-0.137	-0.139	-0.022	0.009	0.245	0.210	-0.020	-0.087	0.049	-0.140	-0.273	0.029	0.365	0.928	0.043	-0.244	-0.616	-0.660	0.202	-0.618	0.081	1.000	
Aerobic stability	-0.129	0.554	-0.139	0.324	-0.181	0.082	0.378	-0.257	0.138	0.130	0.152	-0.283	0.368	-0.089	-0.326	0.142	-0.692	0.371	-0.533	0.098	-0.323	-0.260	1.000

Fig. 5. Heatmap of spearman correlation among response variables of forage-based silage quality assessment. Colors reflect degree of correlation from low (red) to high (blue).
WSC = water soluble carbohydrate; DM = dry matter; CP = crude protein; NDF = neutral detergent fibre; ADF = acid detergent fibre; NH3, ammonia (mg/kg DM); LA, lactic acid; AA, acetic acid; PA, propionic acid; BA, butyric acid; DMD = DM digestibility; CPD = CP digestibility; NDFD = NDF digestibility; LAB = lactic acid bacteria.

Correlation coefficients showed that pH was positively correlated with CP content in legume-based silage ($r = 0.41$) while in forage-based silage, these variables were not correlated ($r = 0.07$). In legume-based silage, concentration of AA, PA, and BA was strongly correlated with NH_3 (mg/kg DM). Similarly, yeast and mould concentration were also positively correlated with NH_3 (mg/total N) with r values of 0.902 and 0.956, respectively. DM and CP digestibility were negatively correlated with pH value, with coefficients of −0.59 and − 0.62, respectively. Additionally, digestibility of CP was positively correlated with concentration of LA ($r = 0.85$) but negatively correlated with AA (r = 0.85). In forage-based silage, pH value was positively correlated with ADF content ($r = 0.513$) while LA was correlated negatively ($r = -0.39$). Positive correlation was also observed in ethanol concentration with WSC and DM loss ($r = 0.59$ and 0.65, respectively).

4. Discussion

4.1. Effect of inoculation rate and type of LAB

The present meta-analysis showed that OF-LAB was the most consistent inoculant in effectively reducing the pH value of silage when applying either in forage or legume silages. This was in agreement with a previous meta-analysis reporting that homolactic LAB decreased pH value regardless of the forage type, LAB strain, and silo type (Oliveira

Table 2
Descriptive statistics of the database used in the meta-analysis.

Response variables	Unit	n	Mean	SD	Min	Max
Chemical composition of legume-based silages prior to ensiling						
Dry matter	g/kg	108	376.3	70.78	229.0	540.0
Crude protein	g/kg DM	62	201.8	40.61	137.0	277.0
NDF	g/kg DM	87	350.4	71.77	222.0	490.0
ADF	g/kg DM	83	256.3	59.87	150.0	374.0
WSC	g/kg DM	85	50.6	32.36	5.5	137.0
Chemical composition of forage-based silages prior to ensiling						
Dry matter	g/kg DM	384	313.0	99.73	131.0	675.0
Crude protein	g/kg DM	300	85.6	31.91	53.9	260.0
NDF	g/kg DM	314	590.9	148.89	257.0	840.0
ADF	g/kg DM	242	343.3	103.3	126.0	517.1
WSC	g/kg DM	174	75.6	65.13	3.9	305.7
Fermentation profile						
pH		549	4.14	0.49	3.1	6.8
NH_3	g/kg DM	164	2.78	3.26	0.18	18
NH_3	g/total N	197	71.14	46.86	3.5	376
Lactic acid (LA)	g/kg DM	561	42.87	32.41	0.1	189
Acetic acid (AA)	g/kg DM	567	16.25	13.76	0.48	76.8
LA/AA		556	3.85	3.33	0.002	26.3
Propionic acid (PA)	g/kg DM	213	4.6	8.99	0.01	54.8
Butyric acid (BA)	g/kg DM	185	2.42	5.14	0.001	32.7
Ethanol	g/kg DM	229	20.05	36.57	0.1	217.8
WSC	g/kg DM	282	13.8	11.45	0.7	56
Chemical composition after ensiling						
Dry matter (DM)	g/kg DM	453	324.48	118.56	126	741
DM loss	g/kg DM	448	5.003	7.78	−38.17	46.7
Crude protein (CP)	g/kg DM	301	116.9	58.88	47.6	311
NDF	g/kg DM	306	501.15	140.61	111.9	839
ADF	g/kg DM	271	303.18	92.81	42.9	527
Digestibility						
DM	g/kg DM	193	642.59	126.18	271	918
CP	g/kg DM	81	642.64	119.87	306	824
NDF	g/kg DM	70	400.35	147.77	151	771
Microbial profile						
LAB	Log CFU/g	367	7.37	1.34	3	11.6
Yeast	Log CFU/g	291	3.94	1.65	0.25	8.8
Mould	Log CFU/g	126	2.42	1.15	0.58	5.5
Aerobic stability	h	170	102.56	8.31	6.9	565

ADF = acid detergent fibre; LAB = lactic acid bacteria; N = number of observation (sample size); NDF = neutral detergent fibre; SD = standard of deviation; WSC = water soluble carbohydrate.

et al., 2017). By contrast, the levels of O-LAB group failed to decrease the pH value, indicating that there may covariates effects. Studies reported that *L. buchneri*, a bacterium belongs to O-LAB, had different effect when applied to substrates differed in the chemical composition (Basso et al., 2018; Kleinschmit and Kung, 2006). This was in agreement with general theory explaining that these two types of inoculants have different fermentation pathways (Muck et al., 2018). Facultative heterolactic and obligate homolactic LAB exclusively produce lactic acid by converting hexoses to lactic acid. Lactic acid is an organic acid with the lowest degree of acid value compared with other organic acids such as acetic acid, propionic acid, and butyric acid (Moon, 1983).

Meanwhile, obligate heterolactic convert portions of lactic acid into acetic acid and 1,2-propanediol during anaerobic fermentation, which have positive effect on aerobic stability due to their antifungal properties (Blajman et al., 2020; Muck et al., 2018). It was evidenced in the present meta-analysis whereas increasing inoculant rate of O-LAB significantly increased the acetic acid and ethanol production as well as improved the aerobic stability while it did not observed with OF-LAB inoculant. Compared with OF-LAB, O-LAB inoculation rate suppressed yeast and increased LAB populations. Many antimicrobial metabolites were detected such as 4-hydroxycinnamic acid, ferulic acid, 3,4-dihydroxycinnamic acid, catechol, azelaic acid, 3-phenyllactic acid, 3,4-dihydroxybenzoic acid, and 4-hydroxybenzoic acid on silage inoculated with *L. buchneri* (Xu et al., 2019a), which may explain that that O-LAB had beneficial effect as antimicrobial inoculant. However, there might different metabolomics profile influencing by O-LAB strains because research exploring this area is limited. Although *L. plantarum* also had such effect, however, our study revealed that OF-LAB failed to suppress the population of yeast and mould. This condition is possible because there might a limited amount of lactic acid produced during fermentation (Cai et al., 2020), where it was confirmed in our study in which the OF-LAB levels had no effect on LA production (Table 3).

4.2. *Effect of enzyme incorporated-LAB inoculants and plant materials for ensiling*

To better understand the inoculants and plant materials effects, we quantified categories of inoculants as discrete variables according to their fermentation pattern and microbial composition. Fermentation profile, changes in chemical composition and digestibility indicated that microbial composition used as inoculants differently affected silage quality of legume and forage-based silages. When applied in legume plants silage, combination of enzyme and LAB (MSE) had no effect on pH while this treatment successfully reduced the pH of forage plants silage. Compared to grass or forage plant, legume plants are more difficult to ensile due to their lower WSC content and higher buffering capacity (Ogunade et al., 2016). However, this study also suggested that both legume and forage based-silage were well-preserved when inoculated with homofermentative LAB either containing single strain (hos-LAB) or multiple strains (hom-LAB) rather than obligate heterofermentative LAB (hes-LAB). This can be seen from the increased of LA production by 43.7% and 41.7%, respectively, for both plant materials. This increase is apparently the reason for the decreasing pH in this type of inoculant, because LA is known to have lower acid value compared with other organic acids such as AA, PA and BA (Moon, 1983). In addition, LA and pH are negatively correlated as shown by the heatmap of spearman correlation (Figs. 4 and 5) in this meta-analysis.

In comparison to other inoculant groups, hes-LAB treatment had superior effect to suppress yeast and mould populations because this type of LAB is well recognized to produce antifungal properties such as acetic acid and propionic acid under aerobic exposure that can contribute to maintain silage quality (Wang et al., 2020; Weinberg and Muck, 1996). As shown in Tables 5 and 6, AA production of hes-LAB treatment was 19.7% and 52.9% higher than that of control group in legume and forage-based silages, respectively. The increased was not happened in other inoculants. The AA increased in hes-LAB promoted to suppress yeast concentration by 20.77% (Table 5) while this effect was not found in hos-LAB and hom-LAB treatments. Decreasing the yeast concentration with comparable increase in LAB concentration in this treatment was beneficial and could be the reason for increasing the aerobic stability by 86.53% (Table 6). A large number of recent publications support this finding (Bai et al., 2020; da Silva et al., 2018; Dong et al., 2020b; Liu et al., 2020). Additionally, this findings was confirmed that AA concentration negatively correlated with yeast ($r = -0.46$) and mould ($r = -0.84$) populations (Fig. 4). Meanwhile, AA and PA were positively correlated with the improvement of aerobic stability (r = 0.15– 0.37) (Fig. 5).

Compared to hom-LAB, MSE had a greater effect in increasing LA production and this evidence partially confirmed the synergistic effect of using enzymes as part of LAB inoculation. In this regard, LA production increased by 58.94% (Table 5). Incorporation of fibrolytic enzymes with LAB inoculants was performed in a study by Zahiroddini et al. (2004) in which the authors found a positive effect on silage quality as well as improved nutritive value of the silage, thus increasing feed efficiency in beef cattle. This is based on a theory that exogenous enzymes are able to

Table 3
Regression model of the effect of inoculant rate of obligate homofermentative and facultative heterofermentative LAB (OF-LAB) on silage quality.

Response variables	Unit	n	Model	Variable estimates				Model estimates		
				Intercept	SE intercept	Slope	SE slope	*P* value	RMSE[a]	AIC[a]
Fermentation profile										
pH		262	L	4.19	0.04	−0.05	0.01	<0.0001	0.223	298.7
NH_3	g/kg DM	75	L	3.24	0.52	−0.89	0.29	<0.01	0.51	326.1
			Q			0.14	0.05	<0.05		
NH_3	g/total N	104	L	78.44	5.69	2.95	11.47	0.798	17.34	1037
Lactic acid (LA)	g/kg DM	269	L	41.38	2.33	1.96	2.05	0.339	11.93	2350
Acetic acid (AA)	g/kg DM	273	L	16.36	0.97	−1.15	0.87	0.189	5.14	1944
LA/AA		268	L	3.39	0.3	0.06	0.37	0.874	30.92	1380
Propionic acid (PA)	g/kg DM	95	L	3.16	0.35	−0.65	0.31	<0.05	1.54	436
Butyric acid (BA)	g/kg DM	81	L	5.12	1.11	−1.24	0.75	0.109	3.63	518.1
Ethanol	g/kg DM	118	L	13.68	3.46	−29.01	2.96	<0.0001	25.41	1096
WSC[a]	g/kg DM	144	L	15.45	1.28	−0.99	1.1	0.371	5.29	1034
Chemical composition										
Dry matter (DM)	g/kg DM	214	L	335.96	10.03	0.07	2.72	0.981	8.50	2130
DM loss	g/kg DM	213	L	3.93	0.6	−0.66	0.31	0.109	2.34	1268
Crude protein (CP)	g/kg DM	149	L	118.65	6.61	−0.87	2.51	0.731	6.10	1354
NDF[a]	g/kg DM	148	L	481.08	14.56	2.44	7.69	0.752	18.20	1613
ADF[a]	g/kg DM	122	L	290.37	9.72	10.66	9.59	0.274	16.96	1284
Digestibility										
DM	g/kg DM	92	L	632.29	21.92	20.18	21.35	0.349	24.92	989.2
CP	g/kg DM	31	L	623.44	32.07	44.39	32.12	0.197	29.84	345.7
NDF	g/kg DM	32	L	465.96	33.3	272.67	34.33	<0.0001	19.10	331.8
			Q			−46.85	5.87	<0.0001		
Microbial profile										
LAB[a]	Log CFU/g	162	L	7.06	0.16	0.19	0.13	0.162	0.71	501
Yeast	Log CFU/g	129	L	4.21	0.18	−0.09	0.14	0.505	0.70	451.2
Mould	Log CFU/g	61	L	2.61	0.201	0.34	0.12	<0.05	0.243	158.6
			Q			−0.06	0.02	<0.05		
Aerobic stability	h	82	L	77.18	12.84	5.62	8.21	0.499	32.93	901.3

[a] WSC = water soluble carbohydrate; NDF = neutral detergent fibre; ADF = acid detergent fibre; LAB = lactic acid bacteria; RMSE = root mean square errors; AIC = Akaike information criterion; L = linear pattern; Q = quadratic pattern.

Table 4
Regression model of the effect of inoculant rate of obligate heterofermentative LAB (O-LAB) on silage quality.

Response variables	Unit	n	Model	Variable estimates				Model estimates		
				Intercept	SE intercept	Slope	SE slope	P value	RMSE[a]	AIC[a]
Fermentation profile										
pH		187	L	4.24	0.05	−0.006	0.06	0.913	0.27	281.3
NH_3	g/kg DM	62	L	3.43	0.54	−0.44	1.82	0.812	25.08	323
NH_3	g/total N	77	L	77.83	6.33	−4.68	37.37	0.905	25.08	788
Lactic acid (LA)	g/kg DM	196	L	41.87	2.55	2.88	3.1	0.358	14.81	1774
Acetic acid (AA)	g/kg DM	199	L	16.48	1.07	3.44	1.38	<0.05	6.70	1493
LA/AA		196	L	3.39	0.19	−0.59	0.31	0.056	1.74	858.5
Propionic acid (PA)	g/kg DM	77	L	3.18	0.85	2.22	0.94	<0.05		495
Butyric acid (BA)	g/kg DM	60	L	5.01	1.26	−1.89	1.21	0.141	4.36	402.3
Ethanol	g/kg DM	94	L	13.75	2.3	5.45	1.24	<0.0001	5.20	732
			Q			−1.00	0.19	<0.0001		
WSC	g/kg DM	116		15.69	1.26	−1.39	0.88	0.124		12.03
Chemical composition										
Dry matter (DM)	g/kg DM	159	L	335.22	11.07	9.62	10.42	0.362	17.89	1770
DM loss	g/kg DM	148	L	4.2	0.71	−0.74	1.02	0.472		996
Crude protein (CP)	g/kg DM	110	L	118.32	5.76	−4.48	3.72	0.245		1079
NDF[a]	g/kg DM	115	L	481.06	14.57	20.98	17.97	0.256	28.05	1327
ADF[a]	g/kg DM	102	L	290.46	9.63	11.23	12.69	0.39	19.55	1102
Digestibility										
DM	g/kg DM	61	L	632.05	21.17	−14.23	15.64	0.374	22.28	688
CP	g/kg DM	28	L	623.56	34	−31.98	14.88	0.069	18.41	310.1
NDF	g/kg DM	21	L	465.98	43.41	144.03	102.39	0.232	45.93	241
Microbial profile										
LAB	Log CFU/g	118		7.06	0.13	0.56	0.18	<0.05	0.93	386
Yeast	Log CFU/g	114	L	4.23	0.18	−0.41	0.17	<0.05	0.74	414.4
Mould	Log CFU/g	56	L	2.61	0.19	0.17	0.61	0.788	0.719	182.4
Aerobic stability	h	75	L	75.58	16.09	54.98	15.9	<0.01	66.97	870
			Q			−6.08	2.36	<0.05		

[a] WSC = water soluble carbohydrate; NDF = neutral detergent fibre; ADF = acid detergent fibre; LAB = lactic acid bacteria; RMSE = root mean square errors; AIC = Akaike information criterion; L = linear pattern; Q = quadratic pattern.

Table 5
Effect of LAB inoculants with or without fibrolytic enzyme on legume based silage quality.

Response variables*	Unit	n	Con	MSE	EN	hes-LAB	hos-LAB	hom-LAB	MS	SEM	p-value
Fermentation profile											
pH		108	4.94a	4.34a	4.66a	4.71ab	4.47b	4.39b	4.67ab	0.047	<0.0001
NH_3	g/kg DM	21	4.30	–	2.69	1.74	1.59	–	–	0.711	0.482
NH_3	g/total N	51	85.68	63.13	77.16	61.46	60.99	73.65	65.53	6.562	0.213
Lactic acid (LA)	g/kg DM	112	41.21b	65.5a	51.17ab	40.04b	52.17ab	59.22a	52.79ab	3.062	0.003
Acetic acid (AA)	g/kg DM	112	23.4b	24.36b	29.93a	28.02a	21.bc	16.51c	20.91bc	1.300	0.011
LA/AA		112	2.37c	2.90c	1.98c	1.60c	3.66b	5.34a	3.58b	0.315	0.003
Propionic acid (PA)	g/kg DM	31	4.77	3.54	4.98	1.41	2.79	3.36	3.32	1.615	0.166
Butyric acid (BA)	g/kg DM	33	9.85	6.74	5.43	4.54	2.96	4.35	4.19	0.895	0.408
Ethanol	g/kg DM	34	2.83b	–	2.42b	7.63a	3.14b	1.96b	–	6.272	<0.0001
WSC	g/kg DM	83	11.56	12.61	11.22	8.78	10.93	10.58	9.73	1.257	0.230
Chemical composition											
Dry matter (DM)	g/kg DM	84	339.9	341.74	341.74	339.84	339.33	339.49	336.9	12.936	0.999
DM loss	g/kg DM	96	2.99	2.82	3.86	2.86	3.16	3.39	2.29	0.794	0.975
Crude protein (CP)	g/kg DM	53	193.89	193.47	194.49	196.61	197.53	190.68	191	8.088	0.865
NDF	g/kg DM	47	406.88a	356.77b	372.24b	385.69ab	367.93b	381.45ab	389.13ab	20.510	<0.001
ADF	g/kg DM	49	301.27a	267.31b	275.82b	294.95ab	280.71b	291.81ab	297.75ab	13.259	0.004
Digestibility											
DM	g/kg DM	49	6.25.43	623.74	603.77	619.61	626.1	631.18	610.79	18.026	0.983
NDF	g/kg DM	37	340.86	–	306.23	307.93	303.25	310.61	355.01	24.293	0.821
LAB	Log CFU/g	68	7.27	7.05	7.61	7.41	6.87	5.94	6.03	0.220	0.340

* WSC = water soluble carbohydrate; NDF = neutral detergent fibre; ADF = acid detergent fibre; LAB = lactic acid bacteria; SEM = standard error of means; CFU = colony forming unit; Con = control (without inoculant); MSE = mixed of LAB + fibrolytic enzymes; EN = fibrolytic enzymes; hes-LAB = heterofermentative LAB (single strain/type); hos-LAB = homofermentative LAB (single strain/type); hom-LAB = homofermentative LAB (multiple strain/type); MS = multiple type of LAB (homofermentative + heterofermentative).

Table 6
Effect of LAB with or without fibrolytic enzyme on forage based silage quality.

Response variables*	Unit	n	Con	MSE	EN	hes-LAB	hos-LAB	hom-LAB	MS	SEM	p-Value
Fermentation profile											
pH		424	4.12a	3.85b	3.91b	4.11a	4.02b	3.90b	4.07ab	0.024	<0.0001
NH_3	g/kg DM	140	3.14	3.09	2.99	3.13	2.75	3.03	3.07	0.276	0.823
NH_3	g/total N	135	86.59	87.21	84.58	58.79	71.24	64.59	81.57	4.033	0.222
Lactic acid (LA)	g/kg DM	432	39.06b	44.21b	41.79b	41.05b	50.54a	55.35a	39.12b	1.559	<0.0010
Acetic acid (AA)	g/kg DM	438	14.98b	16.79b	18.11ab	22.94a	13.51b	13.81b	21.44a	0.657	<0.0001
LA/AA		427	3.52b	4.01b	3.6b	1.93c	5.86a	6.37a	2.48bc	0.161	<0.0001
Propionic acid (PA)	g/kg DM	170	3.86b	2.46b	1.71bc	3.65a	0.37c	–	11.19a	0.690	<0.0001
Butyric acid (BA)	g/kg DM	142	4.23	3.48	3.44	3.77	3.36	3.72	2.16	0.431	0.059
Ethanol	g/kg DM	186	14.29b	13.58b	21.77a	5.31bc	28.99a	19.12a	12.39b	2.681	0.003
WSC	g/kg DM	188	17.51	16.22	17.61	14.73	14.69	14.23	14.22	0.835	0.581
Chemical composition											
Dry matter (DM)	g/kg DM	356	336.52	330.27	329.68	336.39	337.11	336.45	336.83	6.284	0.989
DM loss	g/kg DM	335	4.77	6.37	5.94	6.53	4.61	4.28	5.85	0.425	0.498
Crude protein (CP)	g/kg DM	234	98.2	99.84	103.82	99.29	99.39	107.32	97.84	3.849	0.605
NDF	g/kg DM	245	518.68	509.06	485.53	518.91	512.83	501.21	517.07	8.983	0.126
ADF	g/kg DM	208	304.46	303.75	291.16	298.45	307.31	294.21	306.54	6.435	0.779
Digestibility											
DM	g/kg DM	139	626.12b	639.26b	639.98b	650.26b	619.67b	669.33a	625.04b	10.702	0.039
CP	g/kg DM	68	636.07	652.68	697.17	632.59	655.6	686.53	651.81	14.536	0.285
NDF	g/kg DM	26	514.84b	478.45b	403.6c	536.7b	657.43a	552.99b	521.93b	28.980	0.030
Microbial profile											
LAB	Log CFU/g	31	6.98b	7.29ab	7.27ab	7.73a	7.52a	7.49a	7.92a	0.241	<0.0010
Yeast	Log CFU/g	290	4.43a	4.06a	3.97ab	3.51b	4.23a	4.7a	3.35b	0.097	<0.0001
Mould	Log CFU/g	265	2.66	2.57	2.39	2.15	2.73	2.29	2.37	0.071	0.226
Aerobic stability	h	115	83.12b	103.26ab	108.79ab	155.05a	101.78b	81.96b	149.92a	0.775	<0.0001

* WSC = water soluble carbohydrate; NDF = neutral detergent fibre; ADF = acid detergent fibre; LAB = lactic acid bacteria; SEM = standard error of means; CFU = colony forming unit; Con = control (without inoculant); MSE = mixed of LAB + fibrolytic enzymes; EN = fibrolytic enzymes; hes-LAB = heterofermentative LAB (single strain/type); hos-LAB = homofermentative LAB (single strain/type); hom-LAB = homofermentative LAB (multiple strain/type); MS = multiple type of LAB (homofermentative + heterofermentative).

degrade cell walls and release soluble carbohydrates that are then available for LAB to further convert into lactic acid (Muck et al., 2018). In the present meta-analysis, the positive effects on fibre degradation were confirmed, as the NDF and ADF contents decreased by 12.32% and 11.28%, respectively, whereas this effect was greater than those of other types of inoculants, particularly in legume silage. This is probably because forage plants had higher substrates to be utilized by the enzymes as shown from the chemical composition of the descriptive analysis (Table 2). However, the effect of enzymes when added into microbial inoculants varied depending to which they were paired. This is a limitation of our study as we did not categorize the enzymes either they paired in a homofermentative LAB or obligate heterofermentative

LAB due to small sample size. The discrepancies may also occured when they applied to different type of plant. For instance, in alfalfa silage, *L. fermentum* 17SD-2 + commercial cellulase showed more effect in improving silage quality and nutritive value than LAB inoculant and cellulase when given alone (Su et al., 2019), whereas combination of xylanases and cellulases with LAB inoculant containing *L. buchneri* LN4017, *L. plantarum* LP7109 and *L. casei* LC3200 did not improve overall quality of alfalfa silage (Lynch et al., 2014, 2015). Moreover, the effects also varied with the forage used as substrate (Zhao et al., 2018; Zhang et al., 2020; Dong et al., 2020a). These factors may be applied to explaining why the effect of enzyme addition was not found in forage-based silage in this study. Although there was an explanation suggesting that fibrolytic enzymes would be more effective when applied to low-WSC forages (Guo et al., 2014; Khota et al., 2016), further investigation is still needed to provide a clear insight in this area.

As observed in the forage-based silage in this study, both hes-LAB and hos-LAB similarly had promoting effects on LAB concentration (Table 6). This is possibly because both inoculants, as indicated by previous investigations, have the ability to maintain LAB abundance. For instance, reports show that either combined with *L. plantarum* or not, *L. hilgardii* was effective in maintaining or even enriching the lactobacilli population (Liu et al., 2019; Wang et al., 2020). However, in terms of reducing yeast concentration, hes-LAB inoculant alone or when mixed with hom-LAB (MS-LAB) had greater effect than hos-LAB, hom-LAB or MSE treatments, indicating that obligate fermentative LAB as the aforementioned mechanism is an effective inoculant for antifungal effects, thereby playing an important role in increasing the aerobic stability of silage. In the mixed culture inoculant, the hos-LAB produced large amounts of lactic acid, rapidly reduced the pH and suppressed undesirable organisms, thus maintaining nutrients. At the same time, hes-LAB would maintain the lactic acid concentration and in the open-silo period this type of inoculant produced AA and antifungal compounds, thus improving aerobic stability. A large number of recent publications support this finding (Bai et al., 2020; da Silva et al., 2018; Z. Dong et al., 2020b; Liu et al., 2020).

With regard to enzyme addition to the microbial inoculant, we did not observe any additional benefit on aerobic stability of forage-based silage. Results showed that MSE inoculant could improve aerobic stability, however, the effect was minimal compared with hes-LAB and MS-LAB. It is noteworthy to underline that, in some situations, excessive degradation of cell walls by enzymes has a deleterious effect on aerobic stability because spoilage yeasts and moulds can utilize soluble carbohydrates (Kung and Muck, 2015). Another report also found that inoculant containing a mixed culture of LAB and *Aspergillus niger* produced enzymes that had lower effectiveness in improving aerobic stability than an inoculant containing only LAB mixtures (Zhao et al., 2018). Similarly, co-inoculation with fibrolytic enzymes (xylanase and endoglucanase) into *L. buchneri* or *L. plantarum* inoculants produced no benefit in silage quality, aerobic stability or nutrient digestibility, whereas inoculation with only *L. buchneri* successfully improved aerobic stability (Jin et al., 2015).

In this study, improvements in DM and NDF digestibility were only found in hom-LAB and hos-LAB treatments, respectively. Enzymes when given alone reduced NDF digestibility. Ideally, enzyme addition would increase the nutritive value of silage thus increasing digestibility. However, the digestible fibre components had been degraded during ensiling which excessive WSC then potentially consumed via undesirable clostridia, moulds and yeasts (Jin et al., 2015; Muck et al., 2018), and this left indigestible fractions thus reducing NDF digestibility. This result was supported by decreased NDF content as a result of fibrolytic enzyme treatment as a co-inoculant which plays a role in hydrolyzing hemicellulose and cellulose during ensiling (Jin et al., 2015; Dong et al., 2020b). In previous studies, homolactic LAB or facultative heterolactic LAB showed a positive effect on DM and NDF digestibility (Cao et al., 2011; Liu et al., 2016; Lara et al., 2018a). In their study, Lara et al. (2018b) reported increase in NDF digestibility by 25.8% by using *L. plantarum* as an inoculant. Possible reasons have been proposed, particularly that homolactic LAB or facultative heterolactic LAB were effective in preserving the nutritional value of silage, thus making it available for digestion. Although DM loss was not affected in this study, significant increase in LA content may protect soluble carbohydrates from spoilage, thereby preserving nutrient content of the ensiled forage (Lara et al., 2016; Oliveira et al., 2017).

5. Conclusion

This meta-analysis suggests that increasing inoculation rate for all types of inoculants are effective to improve silage quality regardless types of plants but O-LAB apparently showed more advantages than that of OF-LAB at improving aerobic stability. Incorporation of fibrolytic enzymes into LAB inoculant seemed to be more effective when applied to legume plants silage where there is no additional benefit when inoculated to forage plants silage. Among inoculant groups, hos-LAB and hom-LAB are recommended as inoculants on forage based-silage considering their positive effects on DM and NDF digestibility.

CRediT authorship contribution statement

Agung Irawan: Data collection, investigation, writing - original draft, formal analysis. **Ahmad Sofyan**: Reference collection, rechecking the metadata, manuscript correction, correlation analysis, figure visualization. **Roni Ridwan**: Manuscript correction. **Hasliza Abu Hassim**: Data curation, manuscript correction. **Adib Norma Respati**: Data collection, data input. **Sadarman**: Data collection, data input. **Wira Wisnu Wardani**: Manuscript correction. **Wulansih Dwi Astuti**: Manuscript correction. **Anuraga Jayanegara**: Supervision, conceptualization, data curation, writing – review the manuscript.

Declaration of competing interest

The authors declare that they have no competing interests.

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