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# Quantifying the interactions between dietary fibers and macronutrient digestibility in broiler chickens: The importance of considering fiber solubility

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ABSTRACT

Dietary fibers (DF) have been conventionally considered to limit nutrient utilization in broiler diets. However, the increasing attention towards the use of high-fiber by-products as feed ingredients to reduce costs and environmental impacts requires a better understanding of the role of fibers in the digestion of broiler chickens. Dietary fibers entail a highly heterogeneous group of polymers that differently affect nutrient digestibility. The aim of this study was to collect and analyze the data from published literature related to the inclusion of fibers into standard broiler diets and subsequent effects on digestion. A literature search was performed to find experimental studies that tested the effects of adding high-fiber ingredients on ileal and total tract digestibility of dry matter (DM), crude protein (CP), fat, and starch. A total of 45 studies and 198 experimental treatments were considered for the statistical analyses. For each diet, total DF (TDF), insoluble DF (IDF), and soluble DF (SDF) were calculated based on tabular data of each ingredient. The analysis unit was the effect size of digestibility expressed as the difference between control and treatment diets (% unit). For every digestibility variable, two multiple curvilinear regression models were fitted. Model 1 included the addition of TDF in the experimental diet in relation to the basal diet as a covariate, whereas model 2 included the addition of IDF and SDF as separate covariates. Model 2 better explained the variability in digestibility effect sizes for all nutrients, indicating that the consideration of DF solubility is required to better understand the effects of DF on nutrient digestibility. The inclusion of IDF showed improvements of up to 10 % units in the digestibility of DM, CP, fat, and starch at additional inclusion levels of up to 50 g/kg DM, beyond which the effects became negative. In contrast, the inclusion of SDF showed negative consequences for nutrient digestibility already beyond 20 g/kg DM. In conclusion, DF can affect digestibility of other nutrients in a positive or negative way, depending on DF characteristics and inclusion level. Solubility of DF was found to explain a large part of the variability in digestibility

*Abbreviations:* DF, dietary fibers; IDF, insoluble dietary fibers; SDF, soluble dietary fibers; CDF, dietary fibers of basal diets; DM, dry matter; CP, crude protein; EE, fat; ST, starch; AID, apparent ileal digestibility; ATTD, apparent total tract digestibility; ATTR, apparent total tract retention; GMD, geometric mean diameter; $R^2$, regression coefficient; $R^2$adj, adjusted regression coefficient; RMSE, root mean square error. Δ, difference between basal and treatment diets.

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effects and therefore, we recommend to consider DF solubility in feed formulation. Furthermore, the additional inclusion of up to 50 g/kg DM of IDF to a standard cereal-soybean-based diet can be advised for improving the nutrient digestibility in broiler chickens, whereas the inclusion of SDF should be minimized and not exceed approximately 20 g/kg DM.

## 1. Introduction

Traditionally, dietary fibers (DF) have received little attention in poultry nutrition, being considered a nutrient dilutant and potential antinutritional factor as reviewed by de Vries et al. (2012). The use of by-products from food and oil industries as raw materials for poultry diets is increasing in popularity to alleviate costs, environmental impacts, and dependency on raw material price fluctuations (de Boer et al., 2014; van Zanten et al., 2014). More recent research has demystified the concept of DF, describing it as a functional nutrient with the capacity to modulate the physical characteristics of the feed and the digesta (Mateos et al., 2012; Kheravii et al., 2018; Jha and Mishra, 2021; Lannuzel et al., 2022). Modifying the functional properties of the digesta through the use of DF can affect certain gastrointestinal parameters (e.g., digesta retention time, enzyme secretion, etc.) that can impact the digestion of nutrients.

However, DF include highly heterogeneous polymers in terms of physicochemical properties and their potential effects on nutrient digestibility (Bach Knudsen, 2014) which should be accounted for when formulating broiler diets. One of the main properties used to characterize DF is their solubility in water at room temperature (Choct, 2015). Insoluble fibers (IDF) provide structural properties to the digesta that stimulate gizzard functioning and particle grinding activity, improving the mixture between digesta and gastric juices and thus, improving nutrient digestibility (Svihus, 2011). Some soluble DF (SDF), particularly those from cereals, however, increase digesta viscosity which limits the interaction between feed nutrients and digestive enzymes (Potkins et al., 1991; Smits and Annison, 1996), thus reducing digestibility either by limiting nutrient breakdown or absorption. Although DF solubility can be a good indicator to assess the effects of DF on nutrient digestibility, other physicochemical characteristics of DF (e.g., particle size, material hardness, extract viscosity, etc.) might also contribute to these effects (de Vries et al., 2012).

Several authors have previously reviewed the effects of SDF and IDF on broiler performance, digestive physiology and digestibility, caeca fermentation, gut health, or animal behavior (de Vries et al., 2012; Mateos et al., 2012; Walugembe et al., 2015; Jha and Mishra, 2021; Lannuzel et al., 2022). However, to accurately predict the nutritional values of poultry diets, quantitative estimations of the effects of various types of fibers on macronutrient digestibility are required.

The objective of this study was, therefore, to compile the existing evidence reporting the effects of DF inclusion in broiler diets on nutrient digestibility. More in particular, the following research questions were set: (1) what is the relationship between the inclusion of DF and the digestibility of nutrients? what is the role of (2) DF solubility, (3) DF particle size, and (4) DF source on these relations?

## 2. Material and methods

### 2.1. Literature search and database creation

Literature studies that evaluated the effects of adding fibrous ingredients in broiler diets were searched using the databases Scopus (Elsevier, https://www.scopus.com/), Web of Science (Thomson Reuters Science, https://www.webofscience.com/) and Google Scholar (https://scholar.google.com). The keywords used in these searches were ''broilers'', "poultry'', ''chicken'' + ''fiber'', ''dietary fiber'', ''non-starch polysaccharides'' (NSP), + ''digestibility'', or ''nutrient retention''. The search resulted in a total of 178 articles related to the nutritional evaluation of ingredients with a relatively high content of fibers in broiler diets (> 400 g DF/kg). For inclusion of a study in our database, a number of inclusion criteria were set: (1) studies testing the effect of a fibrous ingredient individually and not a combination of multiple fibrous sources, and including a basal diet in the experimental design; (2) studies that do not include NSP-degrading enzymes in their diets; (3) studies that besides the inclusion of DF, include other experimental factors (e.g., enzyme addition and breed type), were only accepted if digestibility values were presented by treatment, so results from applicable treatments could be selected.

A database was created to store the information related to the animals, diets, and their effects on digestibility. Dietary information included ingredient composition, whereas animal characteristics included the age at the time of measurement, sex, and breed. Apparent digestibility values of dry matter (DM), crude protein (CP), fat (EE) and starch (ST) either at ileal (AID) or total-tract level (ATTD) were also recorded (Table 2).

Due to the high heterogeneity in the methodologies to analyze DF concentrations among studies, the DF contents were calculated for every experimental diet. Soluble NSP, insoluble NSP, and lignin contents were calculated considering the values of individual ingredients reported by Bach Knudsen (2014), Bach Knudsen (1997) and Centraal Voeding Bureau (2021). Total DF (TDF) was calculated as the sum of insoluble NSP, soluble NSP, and lignin; IDF was calculated as the sum of insoluble NSP and lignin; SDF was assumed to be equal to soluble NSP. Additionally, the CP of the diet was similarly calculated based on the CP levels of the individual ingredients reported by Centraal Voeding Bureau (2021) or Feedipedia (https://www.feedipedia.org) to assess the contribution of each ingredient to the CP of the diet, calculated as follows:

$$\text{Contribution of ingredient i (\%)} = \frac{CP_i\ (g/kg\ DM) \bullet\ P_i\ (g/kg)}{CP_d\ (g/kg\ DM) \bullet 10}$$

where $CP_i$ is the CP concentration (g/kg DM) of ingredient i and $CP_d$ is the concentration (g/kg DM) of the diet, $P_i$ refers to the proportion of ingredient i in the diet (g/kg). The calculated CP contribution of the tested fibrous ingredient was used to apply another selection criterion on the data prior to the statistical analysis. The experimental treatments where the tested fibrous ingredient contributed more than 15 % to the total dietary CP were discarded from the database. This condition aimed to isolate the effects of fibers on the observed responses of digestibility from other effects (e.g., change in CP quality). Additionally, data of two experimental treatments from our research group and in process for publication, fulfilled the previous requirements and were also included in the database. After applying the above-mentioned criteria, a total of 45 studies including 195 treatments were accepted to be used in the statistical analysis.

### *2.2. Statistical analysis*

The analysis variables adopted in this study were the digestibility effect sizes, which refer to the difference in digestibility between a control diet and an experimental diet that included a fibrous ingredient. Apparent digestibility or retention of DM (AID of DM and ATTD of DM), CP (AID of CP and ATTR of CP) and EE (AID of EE and ATTD of EE) were considered both at ileal and total tract levels, whereas ST digestibility was only considered at ileal level (AID of ST) due to the lack of data on total tract digestibility.

$$\text{Effect size (\% units)} = \text{Digestibility}_{\text{Treatment}} - \text{Digestibility}_{\text{Control}}$$

A preliminary analysis using random- and mixed-effects models (Tanner-Smith et al., 2016) was performed using the *robumeta* package in R (Fisher and Tipton, 2015; R Core Team, 2021) to assess the contribution of different variables to explain heterogeneity of the effect sizes of digestibility. The variables related to animal characteristics were age (expressed in days), sex (male, female, and mixed-sexed) and breed (specific commercial strains); and feed-related characteristics were pelletization (yes or no), botanical origin of the fibrous ingredient tested (cereals, legumes, cellulose isolates, pectin isolates, and sunflower seeds) and its inclusion level in the diet (expressed in g/kg). From this preliminary analysis, only botanical origin and inclusion level were consistent ($P < 0.1$ in most of effect sizes of digestibility) in explaining variation among the effects of digestibility (data not shown). Further statistical analyses were carried out using the *lm* function in R (R Core Team, 2021). The first objective was to evaluate the effects of increasing levels of TDF in broiler diets on digestibility. The model used for that purpose was as follows:

$$\text{Model 1: } Y = 0 + B_1 \bullet cDF + B_2 \bullet \Delta TDF + B_3 \bullet \Delta TDF^2 + e$$

**Table 1**

Number of publications and experimental treatments testing the effects of inclusion of fibrous ingredients on digestibility.

| Ingredient | Publications | Treatments | Dry matter AID | Dry matter ATTD | Protein AID | Protein ATTR[3] | Fat AID | Fat ATTD | Starch AID | References[1] |
|---|---|---|---|---|---|---|---|---|---|---|
| **Cereal fibers** | | | | | | | | | | |
| Oat hulls | 7 | 40 | 7 | 36 | 7 | 38 | - | 38 | 9 | 13, 14, 15, 16, 17, 19, 33 |
| Rice hulls | 2 | 10 | 4 | 10 | 4 | 10 | - | 10 | 4 | 2, 20 |
| Wheat bran | 5 | 8 | 3 | 1 | 5 | 5 | 2 | - | - | 10, 12, 25, 30, 35 |
| Rice bran | 4 | 7 | 5 | 7 | 1 | 7 | - | 2 | - | 27, 28, 34, 44 |
| Wheat pentosans | 3 | 5 | - | 3 | 2 | - | 1 | 3 | 2 | 6, 11, 7 |
| Rice bran arabinoxylans | 1 | 3 | - | - | 3 | - | - | - | 3 | 3 |
| Wheat arabinoxylans | 2 | 3 | 2 | 2 | 3 | 2 | 1 | - | 1 | 8, 45 |
| Barley hulls | 1 | 2 | - | 2 | - | 2 | - | 2 | - | 2 |
| **Pectin-rich fibers** | | | | | | | | | | |
| Sugar beet pulp | 8 | 34 | 3 | 27 | 10 | 21 | 7 | 21 | 10 | 1, 9, 13, 15, 17, 19, 29, 31 |
| Isolated pectin | 4 | 11 | - | 11 | - | 9 | - | 9 | 1 | 23, 24, 36, 43 |
| **Other fibers** | | | | | | | | | | |
| Cellulose/lignocellulose | 9 | 23 | 7 | 8 | 9 | 5 | 5 | 6 | 1 | 4, 5, 9, 17, 32, 39, 40, 41, 43 |
| Soybean hulls | 4 | 18 | 10 | 8 | 10 | 8 | - | 8 | - | 16, 40, 41, 22 |
| Sunflower hulls | 3 | 12 | 4 | 8 | 6 | 8 | 2 | 10 | 4 | 20, 30, 42 |
| Pea hulls | 2 | 10 | 4 | 10 | 3 | 9 | - | 9 | 3 | 18, 21 |
| Carboxymethyl-cellulose | 2 | 4 | - | - | - | - | - | 4 | - | 37, 38 |
| Cassava pulp | 1 | 3 | - | 3 | - | 3 | - | 3 | - | 26 |
| Sugarcane bagasse | 1 | 2 | - | - | 2 | - | 2 | - | - | 30 |

Aparent ileal digestibility (AID).
Aparent total tract digestibility (ATTD).
Aparent total tract retention (ATTR).
[1]Data from: 1. Abdel-Daim et al. (2020); 2. Adibmoradi et al. (2016); 3. Annison et al. (1995); 4. Bogusławska-Tryk et al. (2016); 5. Cao et al. (2003); 6. Choct and Annison (1992b); 7. Choct and Annison (1992a); 8. Choct et al. (1996); 9. Donadelli et al. (2019); 10. Fang et al. (2022); 11. Fengler and Marquardt (1988); 12. Gómez-Rosales et al. (2022); 13. González-Alvarado et al. (2010); 14. Hetland et al. (2003); 15. Jiménez-Moreno et al. (2009a); 16. Jiménez-Moreno et al. (2009b); 17. Jiménez-Moreno et al. (2010); 18. Jiménez-Moreno et al. (2011); 19. Jiménez-Moreno et al. (2013); 20. Jiménez-Moreno et al. (2019); 21. Jørgensen et al. (1996); 22. Kurul et al. (2020); 23. Langhout et al. (1999); 24. Langhout et al. (2000); 25. Lin and Olukosi (2021); 26. Okrathok and Khempaka (2020); 27. Osunbami et al. (2021); 28. Pereira and Adeola (2016); 29. Pettersson and Razdan (1993); 30. Pourazadi et al. (2020); 31. Razdan and Pettersson (1994); 32. Röhe et al. (2020); 33. Rougière et al. (2009); 34. Sanchez et al. (2019); 35. Shang et al. (2020); 36. Silva et al. (2013); 37. Smits et al. (1998); 38. Smits et al. (2000); 39. Svihus and Hetland (2001); 40. Tejeda and Kim (2020); 41. Tejeda and Kim (2021); 42. Viveros et al. (2009); 43. Wils-Plotz and Dilger (2013); 44. Zhang et al. (2021); 45.Dorado-Montenegro et al. (2024).

where Y is ΔAID of DM, ΔAID of CP, ΔAID of EE, ΔAID of ST, ΔATTD of DM, ΔATTR of CP, or ΔATTD of EE; The intercept of the model was fixed to 0, since at zero inclusion of TDF into a basal diet, the effect on digestibility is by definition also 0. $B_1$ is the slope for the TDF concentration of the control diet (cDF), $B_2$ refers to the linear slope for the inclusion of TDF in the experimental diet compared with the control diet (ΔTDF), and $B_3$ to the curvilinear slope of ΔTDF; e is the random error term.

The second objective was to evaluate the role of DF solubility on the effects of digestibility. The model used for that purpose was as follows:

Model 2: $Y = 0 + B_1 \bullet cDF + B_2 \bullet \Delta IDF + B_3 \bullet \Delta IDF^2 + B_4 \bullet \Delta SDF + B_5 \bullet \Delta SDF^2 + e$

where Y, $B_1$, cDF and e refer to the same elements described in model 1; $B_2$ and $B_3$ refer to the linear and curvilinear slopes for the additional inclusion of iDF (ΔIDF), whereas $B_4$ and $B_5$ refer to the linear and curvilinear slopes for the inclusion of sDF (ΔSDF) into the control diets. Collinearity between ΔIDF, ΔSDF, and cDF was checked, showing regression coefficients ($R^2$) lower than 0.5. The purpose of including the TDF of the control diet as a covariate was to isolate the interactive effects of adding DF to different basal levels of DF.

To assess the influence of the fibrous ingredient types on the effects of digestibility, the dataset was classified into three ingredient categories: cereal fibers, pectin-rich fibers, and other fibers (Table 1). To statistically evaluate the effect of ingredient type on the effects on digestibility, an analysis of variance (ANOVA test) was performed using the *aov* function in R (R Core Team, 2021), where three elements were added into the formulation of model 2: (1) ingredient group, (2) the interaction between ingredient group and ΔIDF and (3) the interaction between ingredient group and ΔSDF. However, for certain digestibility variables and ingredient groups, there were not sufficient experimental treatments to perform this analysis (e.g., only four experimental treatments tested the effects of cereal fibers on AID of EE, and only three experimental treatments evaluated AID of DM using pectin-rich fibers, Table 1).

To evaluate the role of DF particle size in addition to the effects of DF inclusion level on digestibility, a sub-dataset was created only considering the studies that reported the geometric mean diameter (GMD) of the fibrous ingredients tested (Table 3). This sub-dataset was predominantly composed of ingredients rich in IDF and therefore, the following two statistical models were used and compared:

Model 3: $Y = 0 + B_1 \bullet cDF + B_2 \bullet \Delta IDF + B_3 \bullet \Delta IDF^2 + e$

Model 4: $Y = 0 + B_1 \bullet cDF + B_2 \bullet \Delta IDF + B_3 \bullet \Delta IDF^2 + B_4 \bullet GMD + e$

where the intercept was fixed to 0, $B_1$ refers to the slope of cDF. $B_2$ and $B_3$ refer to the linear and curvilinear slopes for ΔIDF. $B_4$ (only for model 4) refers to the slope of GMD and e refers to the error term. Collinearity between ΔIDF and GMD, and normality of the GMD population was checked for every digestibility sub-dataset. The digestibility variables AID of EE and AID of ST were not considered for this analysis due to the low number of observations (Table 3).

To fit models 3 and 4, each observation was assigned a weight proportional to the inverse of its standard error of the mean (SEM). However, experimental observations were not weighed for models 1 and 2. The relative proportion of observations for SDF sources was lower than for IDF sources in our dataset (Table 1), and the SEM reported for SDF sources were commonly higher, typically associated to greater effect sizes, than for IDF sources. Weighing data according to SEM in models 1 and 2 would minimize the contribution of SDF sources to the model, hampering evaluation of the effect of SDF.

To evaluate the goodness of fit of the four models considered, the following statistical parameters were used: $R^2$, the adjusted regression coefficient ($R^2$adj), and the root mean square error (RMSE), decomposed into the error due to bias (ECT), due to regression

**Table 2**
Descriptive statistics of the dataset used to fit models that consider the basal total dietary fiber concentration (cDF) (models 1 and 2), the inclusion of total dietary fiber (ΔTDF) (model 1), insoluble (ΔIDF) and soluble dietary fiber (ΔSDF) (model 2) to predict digestibility effect sizes of dry matter (DM), protein (CP), fat (EE) and starch (ST).

| | | n | Mean | SD | Min | Max |
|---|---|---|---|---|---|---|
| **Digestibility variables (% units)** | | | | | | |
| Δ AID | | | | | | |
| | DM | 49 | 0.9 | 4.44 | −9.0 | 10.3 |
| | CP | 65 | 1.5 | 4.97 | −26.8 | 12.0 |
| | EE | 20 | −2.7 | 13.48 | −55.1 | 10.0 |
| | ST | 38 | 0.2 | 6.66 | −33.7 | 14.0 |
| Δ ATTD/Δ ATTR | | | | | | |
| | DM | 136 | 0.8 | 3.66 | −14.0 | 10.5 |
| | CP | 127 | 2.7 | 3.89 | −14.1 | 11.9 |
| | EE | 125 | 0.5 | 5.89 | −41.7 | 6.4 |
| **Fiber-related variables (g / kg DM)** | | | | | | |
| | Δ TDF | 195 | 30.4 | 20.95 | −19.6 | 116.2 |
| | Δ IDF | 195 | 23.9 | 22.29 | −64.7 | 99.2 |
| | Δ SDF | 195 | 6.5 | 12.24 | −1.8 | 68.4 |
| | cDF | 195 | 109.2 | 27.57 | 23.3 | 205.0 |

Apparent ileal digestibility (AID).
Apparent total tract digestibility (ATTD).
Apparent total tract retention (ATTR).

**Table 3**
Descriptive statistics of the dataset used to fit models that consider the basal total dietary fiber concentration (cDF), inclusion of insoluble dietary fiber (ΔIDF), soluble dietary fiber (ΔSDF) (model 3 and 4), and geometric mean diameter (GMD) (model 4) to predict digestibility effect sizes of dry matter (DM), protein (CP), fat (EE) and starch (ST).

| | | n | Mean | SD | Min | Max |
|---|---|---|---|---|---|---|
| **Digestibility variables (% units)** | | | | | | |
| Δ AID | | | | | | |
| | DM | 29 | 1.9 | 3.81 | −4.81 | 7.41 |
| | CP | 35 | 3.2 | 3.26 | −2.92 | 12.00 |
| | EE | 9 | 4.6 | 3.28 | −0.71 | 10.00 |
| | ST | 21 | 2.3 | 2.21 | −1.90 | 6.60 |
| Δ ATTD/Δ ATTR | | | | | | |
| | DM | 83 | 1.6 | 2.18 | −3.50 | 7.34 |
| | CP | 76 | 3.8 | 2.72 | −3.40 | 9.70 |
| | EE | 79 | 1.9 | 1.98 | −3.10 | 6.30 |
| **Fiber-related variables (g / kg DM unless otherwise noted)** | | | | | | |
| | Δ TDF | 102 | 29.8 | 17.08 | 0.00 | 116.21 |
| | Δ IDF | 102 | 27.3 | 16.32 | 0.00 | 95.70 |
| | Δ SDF | 102 | 2.4 | 3.91 | −1.36 | 20.51 |
| | cDF | 102 | 102.5 | 19.83 | 81.81 | 154.06 |
| | GMD (μm) | 102 | 526 | 221 | 73 | 914.72 |

Apparent ileal digestibility (AID).
Apparent total tract digestibility (ATTD).
Apparent total tract retention (ATTR).

**Table 4**
Sample size (n), equation description and predictive performance ($R^2$, $R^2$adj, RMSE and its decomposition terms ECT, ER and ED, expressed as a percentage of RMSE) of two models that predict the effects of adding total dietary fiber (TDF, model 1) or insoluble and soluble dietary fiber (IDF, SDF, model 2) on the effect size of nutrient digestibility.

| Digestibility variable | Model | n | Equation | $R^2$ | $R^2$adj | RMSE | ECT | ER | ED |
|---|---|---|---|---|---|---|---|---|---|
| ΔAID of DM | model 1 | 49 | 0 + 0.011cDF + 0.038ΔTDF - 0.001ΔTDF$^2$ | 0.18 | 0.13 | 4.05 | 0.3 | 0.1 | 99.6 |
| | model 2 | | 0 + 0.024cDF - 0.012ΔIDF - 2e−04ΔIDF $^2$ - 0.213ΔSDF + 4e−04ΔSDF$^2$ | 0.25 | 0.17 | 3.88 | 0.0 | 0.0 | 100.0 |
| ΔATTD of DM | model 1 | 136 | 0–0.013cDF + 0.209ΔTDF - 0.004ΔTDF$^2$ | 0.34 | 0.32 | 3.04 | 1.6 | 0.6 | 97.8 |
| | model 2 | | 0–5e−04cDF + 0.075ΔIDF - 0.002ΔIDF $^2$ - 0.124ΔSDF - 0.001ΔSDF$^2$ | 0.39 | 0.36 | 2.93 | 0.1 | 0.0 | 99.9 |
| ΔAID of CP | model 1 | 65 | 0–0.014cDF + 0.185ΔTDF - 0.002ΔTDF$^2$ | 0.22 | 0.18 | 4.54 | 0.6 | 0.5 | 99.0 |
| | model 2 | | 0–0.006cDF + 0.138ΔIDF - 0.002ΔIDF $^2$ + 0.101ΔSDF - 0.006ΔSDF$^2$ | 0.61 | 0.58 | 3.20 | 0.1 | 41.6 | 58.3 |
| ΔATTR of CP | model 1 | 127 | 0–0.010cDF + 0.226ΔTDF - 0.003ΔTDF$^2$ | 0.36 | 0.34 | 3.77 | 1.8 | 3.0 | 95.2 |
| | model 2 | | 0 + 0.006cDF + 0.109ΔIDF - 0.001ΔiDF$^2$ - 0.336ΔSDF + 0.006ΔSDF$^2$ | 0.47 | 0.44 | 3.44 | 0.1 | 0.1 | 99.8 |
| ΔAID of EE | model 1 | 20 | 0–0.052cDF + 0.579ΔTDF - 0.008ΔTDF$^2$ | 0.28 | 0.16 | 11.36 | 0.8 | 0.0 | 99.1 |
| | model 2 | | 0 + 0.030cDF + 0.450ΔIDF - 0.006ΔIDF $^2$ - 1.329ΔSDF + 0.030ΔSDF$^2$ | 0.91 | 0.88 | 3.96 | 0.1 | 0.0 | 99.9 |
| ΔATTD of EE | model 1 | 125 | 0–0.058cDF + 0.532ΔTDF - 0.009ΔTDF$^2$ | 0.31 | 0.29 | 4.89 | 2.8 | 0.0 | 97.2 |
| | model 2 | | 0–0.005cDF + 0.329ΔIDF - 0.005ΔIDF $^2$ - 0.036ΔSDF - 0.005ΔSDF$^2$ | 0.68 | 0.66 | 3.34 | 0.1 | 0.0 | 99.9 |
| ΔAID of ST | model 1 | 38 | 0–0.098cDF + 0.427ΔTDF - 0.003ΔTDF$^2$ | 0.58 | 0.55 | 4.26 | 1.5 | 1.2 | 97.3 |
| | model 2 | | 0 + 0.004cDF + 0.272ΔIDF - 0.002ΔIDF $^2$ - 0.130ΔSDF + 0.004ΔSDF$^2$ | 0.81 | 0.78 | 2.86 | 0.2 | 0.0 | 99.8 |

Abbreviations: adjusted regression coefficient ($R^2$adj), apparent ileal digestibility (AID), apparent total tract digestibility (ATTD), apparent total tract retention (ATTR), crude protein (CP), dry matter (DM), error due to bias (ECT), due to disturbance (ED), error due to regression (ER), ether extract or fat (EE), regression coefficient ($R^2$), root mean square error (RMSE), starch (ST).

(ER), and due to disturbance (ED) (Ott and Longnecker, 2015; Ellis et al., 2014).

## 3. Results

### 3.1. The AID and ATTD of nutrients with additional dietary fibers

An overview of the data collected from literature, the relations between DF levels of control and treatment diets and nutrient digestibility are shown in Figure S1 in the Supplementary Materials. The average DF level of the basal diets (i.e., no additional inclusion of DF) was 109 g/kg DM. Basal diets resembled conventional broiler diets, including as major components cereals (maize, wheat, or rice) and a protein source mainly derived from soybean. The additional inclusion of TDF (ΔTDF) typically increased nutrient digestibility until a threshold inclusion level, beyond which digestibility decreased (Figure S2, Supplementary material). In the cases of AID and ATTD of DM, effect sizes were typically positive until ΔTDF levels of 40–60 g/kg DM, reaching values up to 10 % units (Silva et al., 2013; Kurul et al., 2020). For AID and ATTR of CP, positive effect sizes of up to 12 % units (Pourazadi et al., 2020) were reached until ΔTDF levels of approximately 80 g/kg DM, although for ATTR only one experiment reported ΔTDF values greater than 60 g/kg DM. For AID and ATTD of EE, positive effect sizes were observed only until ΔTDF levels of approximately 25 g/kg, except for Röhe et al. (2020) where positive effect sizes were observed up to approximately 40 g/kg DM. For AID of ST, positive effect sizes were reported throughout the whole range of ΔTDF values.

The positive effects on nutrient digestibility with ΔTDF were mainly related to addition of IDF sources; experiments where negative or marginal effect sizes were found at ΔTDF $<$ 40 g/kg DM all tested inclusion of fiber sources rich in SDF (Langhout et al., 1999, 2000; Jiménez-Moreno et al., 2013). Only the study performed by Silva et al. (2013), who tested the addition of isolated pectin, reported positive effects of adding an SDF source on ATTD of DM and ATTR of CP. In studies where one fibrous ingredient was substituted by a different one (Choct et al., 1996; Langhout et al., 1999), thereby changing IDF and SDF concentrations while having little effects on TDF, strong (negative) effects were found at ΔTDF values close to 0. These negative effects sizes at low ΔTDF were particularly prominent for AID of CP, AID and ATTD of EE, and AID of ST.

### 3.2. Statistical models

Model 1 resulted in moderate prediction performance of the digestibility effect sizes for some nutrients, with $R^2$adj ranging from 0.13 in the case of AID of DM to 0.55 for AID of ST (Table 4). However, considering DF solubility by using model 2, considerably improved the prediction performance resulting in higher $R^2$ and $R^2$adj, and lower RMSE. For both model 1 and 2, the major source of error was due to disturbance (random error). The $R^2$adj of model 2 increased in comparison to model 1 from 4 % units in the case of ΔAID of DM and ΔATTD of DM to 72 % units in the case of ΔAID of EE. The inclusion of insoluble DF (ΔIDF) increased nutrient digestibility, as indicated by the positive linear slopes for ΔIDF in model 2, with the exception of ΔAID of DM. The curvilinear slopes of the ΔIDF term were negative for all digestibility variables, representing a concave curve, following the positive effects of ΔIDF on nutrient digestibility until a threshold, beyond which digestibility decreased (i.e., negative effect sizes). In the case of ΔAID of CP, this threshold occurred at ΔIDF values of approximately 50 g/kg DM, whereas ATTD of DM decreased, on average, when ΔIDF was greater than approximately 40 g/kg DM. The negative linear slopes for ΔSDF in model 2 indicate the negative effects of SDF sources on digestibility, except for ΔAID of CP. The ATTD of DM and ATTR of CP decreased up to 15 % units at ΔSDF levels of 40–75 g/kg DM, whereas the effects on AID of EE and ATTD of EE were even more pronounced, showing effect sizes of 40–50 % at 50/kg DM ΔSDF (Choct et al., 1996; Langhout et al., 1999).

When considering the effects of ingredient type and its interactions with ΔIDF and ΔSDF on the digestibility variables via ANOVA analysis, only ΔATTD of DM and ΔATTD of EE showed effects from these covariates ($P < 0.05$). However, from visual inspection of the fitted curves of model 2 for each of the three ingredient types considered, we detected that these interactions were caused by

**Table 5**
Sample size (n), equation description and predictive performance ($R^2$, $R^2$adj, RMSE and its decomposition terms ECT, ER and ED, expressed as a percentage of RMSE) of two models that predict the effects of adding insoluble dietary fiber (IDF, model 3) and the geometric mean diameter (GMD) of the fibrous source (IDF + GMD, model 4) on the effect size of nutrient digestibility.

| Digestibility variable | Model | n | Equation | $R^2$ | $R^2$adj | RMSE | ECT | ER | ED |
|---|---|---|---|---|---|---|---|---|---|
| ΔAID of DM | model 3 | 29 | 0 + 0.006cDF + 0.098ΔIDF - 0.002ΔIDF $^2$ | 0.24 | 0.15 | 3.57 | 1.1 | 0.0 | 98.9 |
| | model 4 | | 0 + 0.067cDF + 0.229ΔIDF - 0.004ΔIDF $^2$ - 0.012GMD | 0.50 | 0.42 | 3.14 | 2.1 | 10.5 | 87.4 |
| ΔATTD of DM | model 3 | 83 | 0 + 0.013cDF + 0.057ΔIDF - 0.002ΔIDF $^2$ | 0.49 | 0.47 | 1.99 | 3.7 | 0.0 | 96.2 |
| | model 4 | | 0 + 0.057cDF - 0.007ΔIDF - 0.001ΔIDF $^2$ - 0.005GMD | 0.63 | 0.61 | 1.73 | 1.1 | 0.1 | 98.8 |
| ΔAID of CP | model 3 | 35 | 0 + 0.035cDF + 0.059ΔIDF - 0.001ΔIDF $^2$ | 0.71 | 0.68 | 3.07 | 8.1 | 0.2 | 91.6 |
| | model 4 | | 0 + 0.042cDF + 0.108ΔIDF - 0.002ΔIDF $^2$ - 0.003GMD | 0.72 | 0.68 | 3.10 | 9.4 | 1.4 | 89.2 |
| ΔATTR of CP | model 3 | 76 | 0 + 0.001cDF + 0.196ΔIDF - 0.002ΔIDF $^2$ | 0.67 | 0.66 | 2.65 | 3.5 | 0.0 | 96.4 |
| | model 4 | | 0 + 0.032cDF + 0.150ΔIDF - 0.004ΔIDF $^2$ - 0.003GMD | 0.70 | 0.68 | 2.61 | 4.2 | 0.1 | 95.6 |
| ΔATTD of EE | model 3 | 79 | 0–0.007cDF + 0.063ΔIDF - 0.001ΔIDF $^2$ | 0.35 | 0.33 | 2.03 | 11.2 | 0.0 | 88.7 |
| | model 4 | | 0 + 0.035cDF + 0.089ΔIDF - 0.002ΔIDF $^2$ - 0.005GMD | 0.48 | 0.46 | 1.84 | 3.2 | 3.1 | 93.7 |

Abbreviations: adjusted regression coefficient ($R^2$adj), apparent ileal digestibility (AID), apparent total tract digestibility (ATTD), apparent total tract retention (ATTR), crude protein (CP), dry matter (DM), error due to bias (ECT), due to disturbance (ED), error due to regression (ER), ether extract or fat (EE), regression coefficient ($R^2$), root mean square error (RMSE), starch (ST).

overfitting of the models to individual data points at high levels of ΔIDF or ΔSDF.

Furthermore, although model 2 showed an improved prediction performance in comparison to model 1 for most nutrients, both models generally underpredicted the positive effects of digestibility that were commonly related to ΔIDF. To get more insight into the variation among the positive effects of the various fiber sources on digestibility in the different studies, model 3 (considering IDF only) and 4 (considering IDF and GMD) were compared for on a subset of studies that reported the GMD of the tested fibrous ingredients. Model 4 showed an improved prediction performance in comparison to model 3 for the variables ΔAID of DM, ΔATTD of DM, and ΔATTD of EE, but not for the variables ΔAID of CP and ΔATTR of CP (Table 5). For all digestibility variables, the slopes of GMD showed negative values, implying that at a specific level of IDF inclusion, greater GMD values decreased the (overall positive) effects of IDF on nutrient digestibility.

## 4. Discussion

The aim of this study was to assess the effects of inclusion level, solubility, and particle size of DF on the digestibility of macronutrients in broiler chickens through a quantitative analysis of published data. The data we gathered showed a great variability of the responses of the gastrointestinal tract (GIT) to the inclusion of DF, and we provided some insights to better understand the causalities involved in such variation. We observed that the inclusion of fibers improved (up to 10 %) or drastically reduced (up to 40–50 %) macronutrient digestibility, depending on inclusion level, solubility and particle size of DF. Taking these DF variables into account allowed to accurately predict the observed effects. Therefore, these findings might be useful when considering DF in the formulation of broiler diets.

To quantify the GIT response to high-fiber diets, the variable adopted in this study was the effect size of digestibility, which refers to the difference in nutrient digestibility between a control (basal) diet and treatment diets that included a fibrous ingredient. The use of this effect size instead of the analysis of absolute digestibility values allowed us to eliminate the variability caused by other reasons not related to the inclusion of fiber, such as the composition of the basal diet. However, interactions among the basal diet and added DF sources may still have influenced the effect sizes of nutrient digestibility (Jiménez-Moreno et al., 2009b; de Vries et al., 2016). Unfortunately, these effects could not be explored in the present analysis due to the scarce variability in the composition of the basal diets in our dataset. Still, to account for this possible interaction, the basal DF level was considered for the prediction of the effect sizes of digestibility in the statistical models.

For the used models, we fixed the intercept element to 0 to satisfy the condition that at extra inclusion levels of DF equal to 0 g/kg, the effects on digestibility also need to be 0. Moreover, the inclusion levels of DF (either TDF, IDF, or SDF) were represented in the models considering both linear and curvilinear elements. The reason for considering a curvilinear element was to allow the prediction of both positive and negative effects on digestibility depending on the extra DF inclusion levels, which is a pattern described by previous reviews (Mateos et al., 2012) and something we visually observed during the phase of data exploration prior to the analysis.

### 4.1. *Effects of total dietary fiber level, solubility and origin on nutrient digestibility*

From fitting model 1 to the data, we observed that ΔTDF showed positive effects on nutrient digestibility until a certain threshold level of ΔTDF was reached, and therefore, higher ΔTDF values caused a decrease in digestibility, which is in agreement with previous findings (Mateos et al., 2012). However, although model 1 predicted positive effects at ΔTDF levels below these theoretical thresholds, there were also observations reporting negative effects on nutrient digestibility. By considering DF solubility in model 2, the prediction error was reduced mainly by better estimating the negative effects on digestibility. These negative effects at relatively low inclusion levels of TDF (lower than approximately 40 g/kg DM) were generally caused by the inclusion of SDF, as shown by their negative slopes in model 2 (Table 4). Contrary, the slopes corresponding to ΔIDF in model 2 showed positive values in most of the digestibility variables, indicating improvements of digestibility until certain ΔIDF levels were reached (40 – 50 g/kg DM). However, model 2 still underpredicted a fraction of the positive effects on digestibility, generally related to the inclusion of IDF. One reason contributing to this underprediction of positive effects (i.e., digestibility improvements) by model 2 was the presence of experimental data reporting negative ΔIDF values or values close to 0, and in general, showing strong negative effects on nutrient digestibility (< 10 % units,). These data points referred to studies that substituted a pure IDF ingredient such as cellulose (assumed to be 100 % IDF), by a pure SDF source, such as isolated pectins or arabinoxylans. Although a decrease of IDF in the diet (i.e. negative values of ΔIDF) might reduce nutrient digestibility, the main reason related to these strong reductions in digestibility was considered to be related to the inclusion of SDF. Therefore, the consideration of these ‘fiber-substitution’ studies in the statistical analysis contributed to reduce the values of the fitted slopes for ΔIDF in model 2, that probably led to such a model underprediction of the positive digestibility effects. Still, these experiments were included in our study to illustrate the effects of ΔSDF at relatively high inclusion levels, otherwise not available in the literature.

Furthermore, another source of variability in the effects of digestibility might be the DF ingredient-specific characteristics, which reflect their polymer composition and physicochemical properties (e.g., water holding capacity, hardness, or extract viscosity). We classified the database into three types of DF ingredients according to their similarity in physicochemical properties and NSP chemical configuration. However, to perform a comparison between these three groups, experimental observations at similar levels of both ΔIDF and ΔSDF are required for each group. Unfortunately, our database did not contain consistent observations of every ingredient group throughout the complete ranges of ΔIDF and ΔSDF, and therefore, conclusions about this source of variation could not be drawn.

### 4.2. Effects of dietary fiber's type on digestive physiology

The effects of DF on digestibility, either positive or negative, are indicative for alterations of the GIT physiology and function. From literature it is known that the different effects on nutrient digestibility observed between ΔIDF and ΔSDF are associated to different alterations of the digesta and digestive processes originating from their distinct physicochemical properties.

The inclusion of IDF provides structural characteristics to the digesta (Svihus, 2011), primarily affecting the organs that mix and grind the feed. The gizzard is considered to be the most sensitive organ to the inclusion of ΔIDF (Svihus, 2011), increasing its grinding activity and relative weight as a result of more intense muscular contractions. Another consequence related to the inclusion of IDF is the increased reflux of digesta from the gizzard to the proventriculus that enhances the mixture of feed materials with HCl and pepsinogen, thus improving protein digestion (Hetland et al., 2005). Hence, these mechanisms may partially explain the increases of AID of CP and ATTR of CP that we observed in our database at IDF inclusion levels of up to 50 g/kg DM. Moreover, Svihus (2011) speculated that stimulating gizzard function also increases the secretion of the satiety hormone cholecystokinin (CCK), which further stimulates pancreatic enzymes secretion, although CCK can also decrease feed intake in broilers (Tachibana et al., 2012). Supporting this speculation, Hetland et al. (2003) reported increases in pancreatic amylase and bile acid concentrations in the jejunum from the inclusion of oat hulls, a highly IDF source. Thus, these mechanisms may be involved in the positive effects on EE and ST digestibilities observed from the extra IDF inclusion in our study.

Similar to IDF, the inclusion of SDF also modifies the physical characteristics of the digesta, although in a very different way, reporting more detrimental effects on macronutrient digestibility compared to the inclusion of IDF, especially on EE digestion. Particularly, the major SDF sources considered in this study (i.e., cereal origin, pectins, and carboxy-methyl-cellulose) exhibit viscous properties; thereby strongly impacting digesta rheology in the GIT (Capuano, 2017). There exists a multifactorial association between highly viscous digesta and the reduction of nutrient digestibility, as reviewed by Smits and Annison (1996). First and most evident, viscous properties impair the contact between digestive enzymes and potential nutrients (e.g., EE) present in the digesta along the GIT (Hardacre et al., 2016), but they can also modify the digesta flow behavior and mean retention time, solute diffusion, and microbial colonization (Smits et al., 1998; Lentle and Janssen, 2010). Additionally, certain types of SDF are able to bind and entrap bile salts, thus reducing the effectiveness in micelle formation and EE absorption (Hemati Matin et al., 2016), although these effects might be dependent on the nature of the EE source (Smits et al., 2000). Therefore, digesta viscosity and bile acid entrapment may partly explain the general detrimental effects that we observed on nutrient digestibility when SDF were included into basal diets. However, SDF from other sources that were not considered in this study (e.g., rapeseed or sunflower meals) contribute little to digesta viscosity (Lannuzel et al., 2022), and therefore, their effects on digestibility may be mediated through other biological mechanisms.

### 4.3. Influence of particle size on the effects of insoluble dietary fibers

The underprediction of the positive effects of IDF on digestibility by model 2 indicates that these effects are not sufficiently explained by the IDF inclusion level only and that other factors such as the structural characteristics of the IDF may help understand its effects on digestibility. It should be acknowledged that the IDF sources considered in this study entail a wide variety of ingredients with distinct fiber-properties. Structural properties that may affect grinding resistance of IDF sources and their mean retention time in the gizzard are for example hardness and particle size (Hetland and Svihus, 2001; Abdollahi et al., 2019). Previous reviews suggested that IDF particle size may be an important factor determining the effects of IDF on gizzard functioning and nutrient digestibility (Svihus, 2011; Mateos et al., 2012). To evaluate this influence, only the publications that reported GMD were used, and the dataset was reduced to scenarios where only high IDF sources were included. Hence, two models were created to fit this sub-dataset: model 3, considering ΔIDF and model 4 including ΔIDF plus GMD. Model 4 better explained variation of ΔAID of DM, ΔATTD of DM and ΔATTD of EE, whereas the effects on protein digestibility (ΔAID of CP and ΔATTR of CP) were not further explained by GMD. The lack of influence of GMD on CP digestibility contradicted our expectations, because several studies found improved gizzard weight, gizzard activity, or both for coarse versus fine IDF sources (Rougière et al., 2009; Jiménez-Moreno et al., 2010; Pourazadi et al., 2020; Tejeda and Kim, 2021), and therefore, we anticipated this would enhance CP digestion. Probably, a potential improvement of AID of CP by the inclusion of coarse IDF might be masked by the increased endogenous losses caused by abrasion of coarse IDF on intestinal mucosa (Montagne et al., 2003). Surprisingly, GMD showed negative slopes for ΔAID of DM, ΔATTD of DM and ΔATTD of EE, indicating that coarseness of IDF might limit the positive consequences of IDF on nutrient digestibility, However, to confirm that fiber GMD may be a limiting factor for digestibility, it would be needed a more balanced dataset testing the effects of GMD of individual IDF sources to avoid ingredient-specific confounding effects (e.g., hardness and water holding capacity).

### 4.4. Practical implications and future perspectives

Instead of being systematically considered as detrimental for diet quality, DF should be seen as a functional nutrient that modulates the physical properties of the digesta with the potential to either improve or impair the nutritional value of the feed, depending on its characteristics and inclusion level. Our results show that the modulation of nutrient digestibility by DF is strongly mediated by its solubility. Therefore, considering not only the TDF level, but also its solubility in diet formulation is strongly recommended to achieve an optimal nutrient digestibility and utilization. The additional inclusion of IDF up to 50 g/kg DM of IDF to a cereal-soybean-based diet can be recommended due to its positive effects on nutrient digestibility. Conversely, formulation strategies that include highly viscous fiber sources are not encouraged although our data suggest that minor additions of SDF up to 20 g/kg DM will not affect digestibility of other nutrients, even in diets without NSP-degrading enzymes. Negative effects of SDF on digestibility might be alleviated by the use of

NSP-degrading enzymes or technological treatments, although the present study did not evaluate their effectiveness.

Such formulation strategies based on specific DF fractions necessitate robust data on the quantity and type of DF present in raw materials. In current feed evaluation systems, DF contents of feed materials are commonly characterized by analyzing crude fiber (CF) or neutral detergent fiber (NDF). Although these procedures are robust with respect to analytical variation (Mertens, 2003), they recover only a part of the DF fraction, largely neglecting SDF. Calculating SDF as the residual fraction remaining after subtraction of several components analyzed by the proximate or Weende analysis system (AOAC, 2000), such as residual NSP (organic matter minus CP, EE, ST, sugars, and NDF), may partially overcome this issue, but still suffers from inaccuracies and accumulation of the analytical errors associated with the constituent analyses. Instead, for routine purposes TDF, IDF, and SDF could be quantified using standard methods developed for the evaluation of foods (AOAC, 2009.01, 2011.25). Alternatively, one could rely on values reported for common feed materials in food and feed databases and scientific literature; the approach chosen for the current study. In the future, apart from DF solubility, such characterizations could be extended to other physicochemical characteristics such as hardness, particle size, gelling- and hydration properties, fermentability, or bulk-providing properties to more accurately predict the fate of DF in the bird's gastrointestinal tract.

This study focused on the digestive consequences of increasing DF, and hence, the impacts of DF level and solubility on feed intake or performance parameters were not considered, and the recommendations provided in this study should be considered only in the light of nutrient digestibility. Further meta-analyses are needed to study and quantify performance responses to the addition of DF. Nevertheless, recommendations from the current study may help to maximize nutrient digestibility and increase utilization of fibrous by-products for poultry diets.

## 5. Conclusions

Considering the data collected from the literature, the inclusion of DF to broiler diets can be presumed to provoke changes in the digestive physiology, that were reflected in the digestibility of nutrients. Dietary fibers can affect digestibility of other nutrients in a positive or negative way, depending on DF characteristics and inclusion level. We could infer that, overall, digestibility showed a curvilinear response to the inclusion of DF, improving at low or moderate levels of DF inclusion, but decreasing at greater levels of DF added.

In addition to the DF inclusion level, the effects on digestibility were greatly influenced by the properties of the added fibers. Depending on solubility, DF modulates the physical properties of digesta where insoluble fibers (IDF) are typically more beneficial for digestion than soluble fibers (SDF). The additional inclusion of IDF at levels up to approximately 50 g/kg DM in a standard cereal-soybean based-diet stimulates the development and function of digestive organs (e.g., gizzard) and thus improves the digestibility of nutrients to levels of up to 10–12 %. Differently, sDF, even at low inclusion levels of approximately 20 g/kg DM modulate digesta viscosity, reducing digestibility up to 40–50 %, especially in the case of fats. All in all, adding IDF can be recommended in broiler feed formulation to maximize nutrient digestibility of standard broiler diets, whereas the inclusion of SDF is not encouraged. As solubility of DF was found to explain a large part of the variability in digestibility effects and therefore, we recommend to consider DF solubility in feed formulation.

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## CRediT authorship contribution statement

**Sonja de Vries:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Alberto Conde-Aguilera:** Funding acquisition, Supervision. **Marta Pérez de Nanclares**: Supervision, Validation, Visualization, Writing – review & editing. **Gonzalo Vivares:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft.

## Declaration of Competing Interest

GV and SV declare no conflict of interests. MPN and ACA were employees of Adisseo France SAS during execution of the meta-analysis.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.anifeedsci.2025.116241.

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