Seed yield and quality responses of oilseed crops to simulated nitrogen deposition: A meta-analysis of field studies

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Abstract
Oilseed crops are widely planted and are closely associated with human nutrition and health. Globally, increased nitrogen (N) deposition has a significant impact on agricultural production; however, in-depth knowledge of oilseed crop yields and quality is still lacking. Here, we performed a global meta-analysis from 128 published papers with 462 paired observations to evaluate the response of oilseed crop yields, yield composition, protein, and oil content to simulated N deposition. The meta-analysis showed that simulated N deposition significantly increased oilseed crop yields in a dose-dependent and duration-dependent manner. The yield compositions were also changed by N deposition, where pod numbers per plant (PNP) and seed weights per pod were significantly increased. Interestingly, our analysis identified PNP as the key factor determining the oilseed crop yield response to simulated N deposition. Additionally, the form of N deposition had no striking influence on either yields or yield components, whereas differences in the sensitivity in rape responses reflected differences in crop species. In terms of oilseed crop quality, although simulated N deposition increased the seed protein content in a dose-dependent manner, there was a significant negative impact on the seed oil content. Furthermore, this negative correlation between seed oil content and biomass under simulated N deposition implies adverse effects caused by a dilution effect. Overall, our results suggest discrete responses of oilseed crop yield, seed protein and oil content to simulated N deposition. This study has ecological and biological implications for oilseed crop yield and quality responses facing global N deposition.

KEYWORDS
classification factors, effect size, global N deposition, oil content, oilseed crops, protein content, yield and yield components
1 INTRODUCTION

Oilseed crops are cultivated throughout the world for their edible oils and applications as biofuels and industrial bioproducts, especially in the light of increased global population growth and dwindling fossil fuel resources (Attia et al., 2021; Hossain et al., 2019). Soybean (Glycine max [L.] Merrill), peanut (Arachis hypogaea L.), oilseed rape (Brassica napus L.), oilseed sunflower (Helianthus annuus L.), and sesame (Sesamum indicum L.) are the most widely grown oilseed crops with the majority of plant oils produced from these crop species (Chen et al., 2019; Dyer & Mullen, 2008; Herridge et al., 2008). Equally important is the nutritional value of their seeds, which can affect human health by providing nutrients such as protein and fatty acids (Lu et al., 2011; Msanne et al., 2020; Zafar et al., 2019). Given their health and economic significance, there is an increased demand for oilseed crop production (Gupta & Gupta, 2016; Harwood et al., 2013) and the challenges brought about by increasing human population and globalization require the production of high-quality seeds, which is dependent on sufficient crop yield.

Since the turn of this century, both fossil fuel and N fertilizer usage has increased dramatically in conjunction with scientific and technological progress (Ackerman et al., 2019). This has driven global N deposition, profoundly influencing ecosystem stability and biogeochemical cycles. On the one hand, the annual increases in N deposition, somewhat surprisingly, has benefitted the green revolution in agriculture as most crops are N-loving plants (Bobhink et al., 2010; Nowlan et al., 2014; Wang et al., 2019). On the other hand, N deposition is a recognized threat to multiple aspects of the biosphere that ultimately impact crop yields and quality (Phoenix et al., 2006; Scheible et al., 2004; Stulen et al., 1998; Wooliver et al., 2018). Therefore, predicting the influences of global N deposition on seed yield and component accumulation has vital ecological and agronomic value.

Generally, N deposition increases oilseed crop yield because N is a vital nutrient element for plants. However, increased N levels may have an inhibitory effect on seed yield which would also occur when excessive N application or specific N forms are used (Basal & Szabó, 2019; Ruiz Diaz et al., 2009). Notably, the combined effects of pod numbers per plant (PNP), seed numbers per pod (SNP), and hundred-grain weight (HGW) determine the oilseed crop yield; therefore, the responses of these yield-influencing component factors need to be explored to understand the major determinants for seed yield under conditions of globally increased N deposition (Bouchet et al., 2014; Diepenbrock, 2000). The responses of seed composition, including protein and oil contents, to increased N are poorly understood. Although N has been widely reported to positively influence protein accumulation (Al-Hadeethi et al., 2019; Šiaudinis & Butkutė, 2013), the specific changes caused by the rate and form of N deposition, as well as the influence of crop species, are still unclear. Interestingly, different studies have shown different pictures when it comes to the seed oil content. For instance, Mason and Brennan (1998) found that N deposition affected the seed oil content of oilseed rape differently depending on where the plants were grown. Another report described variations in oilseed oil content over a period of years under the same N deposition conditions (Šiaudinis & Butkutė, 2013). However, Li et al. (2014) reported that N deposition significantly reduced the seed oil content in oilseed rape. A detailed study by Shakeri et al. (2016) found that N deposition significantly decreased the saturated fatty acid content while significantly increasing that of unsaturated fatty acids in sesame seeds. These findings collectively indicate the complexity of oilseed crop yield and quality responses to global N deposition, as well as the difficulties inherent in a single experiment attempting to understand the overall response.

Meta-analysis has been widely adopted for assessing plant biological and agricultural responses to global environmental changes. Notably, such an approach has been performed in the responses of grain yields and quality to environmental changes (Al-Hadeethi et al., 2019; Rotundo & Westgate, 2009). This has not, however, been done to analyze the oilseed crop yield and quality responses to N deposition. Besides, even though N has shown positive effects on the grain yield of oilseed crops, it is still not clear which yield component is the most relevant factor in response to N deposition. Overall, previous research has been limited in scope and did not relate changes in time, strength, and patterns of N deposition on seed composition.

To address these issues, this study used a pairwise meta-analysis approach to quantitatively assess the impact of N deposition on the grain yield, yield components, and seed nitrogen content in oilseed crops on a global scale. We compiled a database containing 128 publications and 462 studies from around the world. We specifically examined the relation and regulation mechanisms between the seed oil and protein content under conditions of simulated nitrogen deposition. We hypothesized that: (1) N deposition increases the grain yield and protein content in oilseed crops, and that this effect is influenced by the type of crop, as well as by the forms and concentrations of N deposition. (2) N deposition decreases the seed oil content in oilseed crops. (3) The changes in plant biomass show the potential relationship between the seed oil and protein content under N deposition conditions.
2 MATERIAL AND METHODS

2.1 Data collection

Peer-reviewed journal articles published from 1990 to 2020 that reported the oilseed crop yield and quality responses to simulated N deposition were identified using the Web of Science (http://www.isiknowledge.com/). The search terms were “(nitrogen deposition OR nitrogen application OR nitrogen fertilization OR nitrogen nutrition OR nitrogen addition OR nitrogen input) AND (soybean OR peanut OR rape OR sunflower OR sesame) AND (seed) AND (yield OR quality OR protein OR fatty acid OR oil).” Further, studies included in the further meta-analysis had to meet the following criteria: (1) the simulated N deposition experiment was conducted in the field rather than in pots or hydroponic conditions; (2) the N deposition was simulated using inorganic N fertilizer rather than organic N fertilizer due to the latter’s complex composition; (3) the selected experiment was conducted in the field rather than in pots or hydroponic conditions; (4) the means and sample replicates (n) could be derived from the results, and the standard deviation or standard error value for each data set should also be recorded if available; (5) the most recent study should be selected if more than one publication reported results from the same experiment; (6) data from the most recent sampling time should be recorded if a study contained results from various sampling dates; and (7) a study using specific variables should be recognized as an individual study if a study reported other variables, such as crop cultivars and irrigation regimes, besides the simulated N deposition. In addition, results were labeled as REF-ZERO if the study used the treatment without N deposition as a control and were labeled as REF-LOW if the study used the lowest nitrogen deposition treatment as a control.

In total, 128 published papers (Table S1) with 462 individual studies were included. The experimental sites were plotted by summarizing latitude and longitude parameters (Figure S1a). The experimental sites were distributed more than 36 countries throughout the world, with China, the USA, Iran, Canada, and Poland contributing the most (Figure S1b). The complete database contained seven main parameters, namely, seed yield, PNP, SNP, HGW, seed total N content (TN), seed protein content, and seed oil content, as well as other five affiliated indicators, namely, HI, Pn, SPAD, nodule numbers per plant (NNP) and nodule weight per plant (NWP) in legumes. The entire dataset was further divided to illustrate the responses of oilseed crop yield and quality responses to simulated N deposition under different classification factors. For instance, the studied plant species were recorded and divided into “rape,” “soybean,” “sunflower,” “peanut,” and “sesame.” The database was also divided into subgroups entitled “REF-ZERO” and “REF-LOW” according to the simulated N deposition rate of the control treatment. In addition, due to the diversity of the forms of simulated N deposition, we classified the database into “urea,” “ammonium,” “nitrate,” “ammonium and nitrate,” “combined form,” or “unknown.” Furthermore, the influences of simulated N deposition duration and rate were also investigated categorically and continuously.

2.2 Data analysis

2.2.1 Meta-analysis

The simulated N deposition induced effect sizes of the different parameters in our study were assessed using the response ratio (RR) method, according to Han et al. (2020). RR was calculated as the natural logarithm of the ratio between the means of the control ($x_c$) and simulated N deposition ($x_t$) groups, with the following equation:

$$RR = \ln \left( \frac{x_t}{x_c} \right) = \ln(x_t) - \ln(x_c)$$

The results were then transformed into the percentage change, using the formula below, for a better interpretation:

$$\text{N deposition effect (\%) } = \left( e^{RR} - 1 \right) \times 100$$

Generally, effect sizes in a meta-analysis can be weighted by the inverse of pooled variance or replications, which depends on the integrity of the reported standard deviations in the database (Ainsworth & Long, 2005; Lam et al., 2012; Xia et al., 2017). In this study, the replication-based weighting function was employed for assessing the effect sizes due to the absence of standard deviations in most of the included studies, using the following equation:

$$\text{Weight} = \frac{n_t \times n_c}{n_t + n_c}$$

where $n_t$ and $n_c$ represent the number of replicates of the simulated N deposition and control groups, respectively.

Next, the mean effect sizes and 95% confidence intervals (CI) were generated using the software MetaWin Version 2.1 (Sinauer Associates Inc.), by a bootstrapping procedure with 4999 iterations (Rosenberg et al., 2000; Xia et al., 2017). A fixed-effects model was necessary here
to implement valid bootstrapping due to the replication-based weighting function and bootstrapping procedure used in evaluating the effect size or mean effect size (Chung et al., 2013; Lam et al., 2012). Equally important, our study met the criteria for a fixed-effects model (Borenstein et al., 2010) and this model has been adopted in similar meta-analyses (Al-Hadeethi et al., 2019; Zhou et al., 2020), supporting the use of the fixed-effects model in our study. Then, the results were plotted in SigmaPlot 12.5 (SYSTAT Software Inc.), and the effect size of the simulated N deposition was regarded as significantly different from the control if the CI did not overlap zero in each plot.

Furthermore, in assessing the influence of categorical variables on the simulated N deposition induced effect on a certain parameter, bootstrapping was again performed through MetaWin Version 2.1, as described above. However, when considering the correlations between the effect sizes of the studied parameters and continuous variables, including the simulated N deposition rate as well as duration, R software was used to conduct the meta-regression analysis (Liang et al., 2020). The influence of the continuous variable was considered significant when \( p < 0.05 \).

### 2.3 Graphical vector analysis

Graphical vector analysis (GVA) was conducted to assess the presence of “excess synthesis” or “dilution effect” for seed protein and oil contents caused by biomass changes under conditions of simulated N deposition. The GVA was performed according to Koricheva (1999) and Sun et al. (2020). The RR of the compound accumulations and concentrations were plotted on the x and y-axes, respectively, with the biomass taken as the virtual z-axis. The reference point (0, 0) represents the control data while the points indicate the data of responses under simulated N deposition. The contributions of “excess synthesis” or “dilution effect” were then determined by the quadrant location of the data (points in the first quadrant represent excess synthesis while those in the fourth quadrant represent a dilution effect).

### 3 RESULTS

#### 3.1 Overall effects of simulated N deposition on the seed yield, yield components, and the contents of total N, crude protein, and oil in oilseed crops

Across the entire dataset, simulated N deposition significantly increased the seed yield (37.8%) of oilseed crops, as well as the total seed N content (13.4%; Figure 1).

Simultaneously, simulated N deposition significantly increased the HI (16.9%), Pn (11.9%), and SPAD value (9.2%) of these oilseed crops (Figure S2a). In terms of crop yield components, simulated N deposition significantly increased PNP (40.6%) and HGW (5.7%) but did not significantly influence the SNP. In terms of crude protein and oil, significantly increased seed protein contents (7.6%) and decreased oil contents (−2.9%) were observed (Figure 1).

The relationship between the seed N content and the seed yield, protein, and oil contents were also plotted in relation to N deposition (Figure S3). Significant positive linear correlations were found between the seed N content and the seed yield \( (R^2 = 0.547, p < 0.001) \) or protein content \( (R^2 = 0.850, p < 0.001) \). However, a significant negative linear relationship \( (R^2 = 0.814, p < 0.001) \) was observed between seed N content and oil content.

#### 3.2 Effect of simulated N deposition on the seed yield of oilseed crops in response to different classification factors

Numerous factors could influence the overall positive effect of simulated N deposition on oilseed crop yield. These effects differed amongst different crops, and significantly higher yield responses to simulated N deposition were observed in rape (52.8%) and sesame (67.0%) compared with soybean (16.1%) and peanut (36.8%; Figure 2). Besides, simulated N deposition strikingly reduced the NNP
The reference N deposition rate in the data sets also had a significant influence on seed yield responses, with a significantly higher value in the REF-ZERO group (41.2%) than the REF-LOW group (27.0%). In terms of N deposition forms, urea induced significantly higher seed yield responses (53.3%) compared with ammonium-N (31.8%), nitrate-N (20.4%), and ammonium nitrate-N (18.4%), whereas no significant difference was seen among ammonium-N, nitrate-N, and ammonium nitrate-N. Seed yield responses to simulated N deposition were also influenced by the duration of N deposition, and the yield responses were significantly higher when the N deposition lasted for more than 3 years (48.9%) compared with <1 year (30.7%). However, the correlation between the duration of N deposition and the seed yield response is extremely weak (Figure S4a, $R^2 = 7.582e-5$, $p < 0.001$). Considering the N deposition rate, continuously enhanced seed yield responses were observed as the N deposition rate increased. A significant positive linear correlation was obtained (Figure S4b, $R^2 = 0.0449$, $p < 0.001$).

3.3 | Effect of simulated N deposition on the yield components of oilseed crops in response to different classification factors

The responses of the oilseed crop yield components were also impacted by different classification factors. Interestingly, the response of PNP under various classification factors was similar to that of seed yield (Figures 2 and 3), with a higher response in rape (62.9%) compared with peanut (35.3%) and soybean (6.3%), in the REF-ZERO group (48.1%) compared with the REF-LOW group (22.7%), and with N in the form of urea (71.9%) rather than ammonium and nitrate (24.2%). In addition, the PNP responses were higher when the N deposition duration lasted for more than 1 year compared with those lasting for 1 year, with no significant positive correlation observed between the simulated N deposition duration and PNP responses (Figure S5a, $R^2 = 0.0174$, $p = 0.2985$). However, a positive linear relationship was found between PNP responses and N deposition rates (Figure S5b, $R^2 = 0.0659$, $p < 0.05$). In terms of SNP, no significant differences were seen among the different classification factors (Figure 3b). Interestingly, a higher SNP response was observed when N deposition duration lasted for more than 2 years compared with that for 2 years, whereas no significant correlation was obtained between SNP responses and N
deposition duration (Figure S5c, $R^2 = 0.0572, p = 0.1801$). Furthermore, neither classification comparison nor correlation analysis resulted in significant changes in SNP in relation to N deposition (Figure 3b, Figure S5d). The HGW responses to simulated N deposition were consistent among different classification factors, although the responses of rape (4.1%) and soybean (3.8%) were lower than those of sunflower (11.1%), peanut (10.5%), and sesame (16.9%) due to the small amount of collected data (Figure 3c). No significant correlations were observed between HGW responses and simulated N deposition duration and rate (Figure S5e,f).

The correlations between seed yield and yield components of oilseed crops in response to simulated N deposition were further analyzed (Figure 4). The oilseed crop yield changes caused by simulated N deposition were significantly positively correlated with PNP ($p<0.001$). However, no significant relationship was observed between seed yield responses and either SNP or HGW responses (Figure 4).

### 3.4 Effect of simulated N deposition on the seed protein and oil contents in oilseed crops in response to different classification factors

The responses of seed protein content to simulated N deposition were influenced by the crop species, with a higher effect value observed in rape (11.3%) and sunflower (11.5%) than in soybean (1.1%; Figure 5a). The data in the REF-ZERO group (8.5%) showed a significantly larger response to simulated N deposition than those in the REF-LOW group (4.2%). The responses of seed protein content did not show significant differences in terms of N deposition forms, although urea application induced a greater effect (10.8%) than ammonium and nitrate (3.9%). While no significant changes were observed among different experimental durations higher N deposition rates resulted in greater effects (Figure 5a) and a significant positive correlation was observed between the N deposition rate and the seed protein response (Figure S6a, $R^2 = 0.1578, p < 0.001$).

In terms of the seed oil content response to simulated N deposition, no significant differences were observed among the different classification factors (Figure 5b). Although a higher N deposition rate was found to induce a greater negative effect on the seed oil content, the correlation between the two was not significant (Figure 5b, Figure S6b, $R^2 = 0.0137, p = 0.0886$).

### 3.5 Effect of simulated N deposition on the total protein and oil accumulation in oilseed crop and the contribution of seed yield in terms of protein and oil content

As the critical indicator in evaluating oilseed crop productivity, the total protein and oil accumulation were also calculated here by multiplying the seed yield and protein or oil content (using the corresponding data from the same report). Simulated N deposition significantly increased both total protein and oil accumulation by 43.2% and 32.9% respectively (Figure S7).

In addition, a significant positive linear correlation was exhibited between seed yield and protein content in response to simulated N deposition (Figure 6a), which was not seen between seed yield and oil content (Figure 6b). GVA was also conducted to analyze the contribution of seed yield to the protein and oil content (Figure 6c,d). Considering the seed protein responses, 83.2% of the statistical data showed an “excess synthesis.” However, in the analysis of the seed oil content, only 26.8% of the
statistical data showed “excess synthesis” while the proportion showing “dilution effect” (64.9%) correspondingly increased.

4 | DISCUSSION

With the increasing human population and the intensifying of city urbanization, the scale of N deposition is likely to increase in the foreseeable decades, which will have considerable impacts on plant physiology and metabolism (Stevens et al., 2018; Sun et al., 2020). Oilseed crops are a large family of plants that are closely associated with human health and nutrition (Abiodun, 2017); thus, evaluating and predicting their seed yield and quality responses to global N deposition has great ecological and agronomic significance. The principal findings of our meta-analysis were as follows: (1) simulated N deposition increases the leaf Pn, seed N content, and HI of oilseed crops and, thus, positively influences seed yield; (2) simulated N deposition has distinct effects on oilseed crop quality, seen specifically in significantly increased protein content but decreased oil content; (3) the responses of oilseed crop seeds in terms of yield and quality to simulated N deposition were driven by multiple factors, including the crop species and N deposition rate, as well as duration of N deposition. These results advance our understanding of the global patterns of simulated N deposition on the seed yield and seed quality in oilseed crops.

Across the whole data set, simulated N deposition significantly increased the seed yield together with the accumulation of total seed N in oilseed crops (Figure 2). These results, on the one hand, suggest an overall stimulation of net N uptake as a result of simulated N deposition, and, on the other hand, reflect a reduction in the loss of easily metabolized substrates, such as amino acids, ammonia, and nitrate nitrogen (Ackerman et al., 2019; Cabello et al., 2019). Globally, seed yield relies heavily on the supply of exogenous N. Thus, simulated N deposition enhanced Pn (Figure S2a) would be critical to advancing seed yield (Simkin et al., 2020; Wu et al., 2019). Equally, higher N translocation rates from vegetative organs to reproductive organs could also contribute to increase seed yield, as evidenced by the enhanced HI by simulated N deposition (Figure S2a; Heuermann et al., 2021; Xing et al., 2019). Interestingly, simulated N deposition significantly increased the seed protein content but decreased the oil concentration (Figure 2). Previously, Mao et al. (2018) found that simulated N deposition increased the N allocation to soluble protein and free amino acids in foliage but decreased the contents of other nutrient components. This finding suggests that simulated N deposition results in a nutrient imbalance, borne out by the observation that crop yields are determined by the accumulation of excess soluble protein and amino acids rather than oil (Chen et al., 2019; Gao et al., 2020; Herridge et al., 2008). Collectively, the results indicate that simulated N deposition can significantly increase oilseed crop yield and protein content by increasing physiological N accumulation.

In addition, the yield responses to simulated N deposition varied among the different classification factors. Considering the crop species, a higher yield response to simulated N deposition was detected in rape and sesame than in soybean and peanut (Figure 2). This might not be
accidental in that excessive N deposition in legume crops such as soybean and peanut might not contribute to the induction of seed yield. This may be explained by the beneficial effect on plant N acquisition from the biological nitrogen fixation of symbiotic *Rhizobia* (Hauggaard-Nielsen et al., 2016; Kakraliya et al., 2018; Meena et al., 2013). Specifically, the symbiotic *Rhizobia* would affect plants living in an environment with reasonably adequate N and would inhibit direct N uptake by root and thus weaken the positive effect induced by N deposition (Wang et al., 2016). Simultaneously, externally applied N would strongly inhibit nodule formation (NNP and NWP, Figure S2c) and *Rhizobia* nitrogenase activity to conserve energy resources, which eventually resulted in the partial reduction of the N fixation efficiency of nodules (Gan et al., 2003; Nishida & Suzaki, 2018). These together
induced the insensitivity responses of legumes than non-legumes to increased N deposition. Besides, in terms of the form of N deposition, urea induced higher seed yield responses than other forms of N (Figure 2). Urea is an organic nitrogen compound with excellent solubility, high nitrogen content, and fewer destructive effects to the soil, and can be degraded by urease, an important hydrolytic enzyme (Tan et al., 2000; Zhao et al., 2018). Reports have indicated that urease activities are invariably higher than other soil N cycle enzymes when the plants are growing under abiotic and biotic stresses (Akiyama et al., 2013; Mavi & Singh, 2007; Sher et al., 2013). These observations partially explain the superiority of nitrogen deposition in the form of urea and stress the importance of soil ecological features for plant responses to environmental changes (Jansson & Hofmockel, 2020). However, no significant differences in either seed yield or yield components were observed between ammonium and nitrate N deposition (Figures 2 and 3), indicating that N concentration rather than N form is the main driving factor determining oilseed crop yield. This conclusion is strengthened by the significant positive correlation observed between oilseed crop yield responses and simulated N deposition, in terms of both rate and duration (Figure S3). Additionally, oilseed crops are undergoing a transition to total nitrate nutrition due to the excessive activity of soil nitrifying bacteria in dryland crops (Subbarao et al., 2015, 2021). Therefore, the influence of different forms of nitrogen deposition will be partially undermined by soil microorganisms, and these should be explored in future experimental studies.

The crop yield components are important when further analyzing the causes of changes in oilseed crop yields, given their roles in determining crop yield (Sadras & Slafer, 2012; Slafer et al., 2014). Specifically, our results showed that the PNP, rather than the SNP or HGW, was positively correlated with the crop yield response to simulated N deposition (Figure 4). This is supported by the significant effects on the PNP by the different classification factors, in contrast to the SNP or HGW (Figure 3). This may be a result of the essentially constant responses of both the SNP and HGW to N deposition in the growth phase compared with that of the PNP (Fageria & Santos, 2008). In line with this is the documented importance of PNP in determining oilseed crop yield in response to other environmental factors such as light density, UV-B radiation, and atmospheric carbon dioxide concentration (Kumagai et al., 2015; Liu et al., 2012, 2013). Moreover, the positive relationship between N addition and PNP formation has been attributed to the regulatory role of cytokinin (Kambhampati et al., 2017; Schwarz et al., 2020). In this respect, the plasticity of PNP renders it a significant factor in determining crop yield, but this evaluation should be combined with the plant growth phases as well as the simulated N deposition rate. Also, traits related to the PNP should be considered in future oilseed crop breeding. Collectively, the above findings showed that, although simulated N deposition can promote oilseed crop yield, this effect is also controlled by many additional factors such as rhizobia inoculation, soil microbial ecology, and internal physiological regulation. These findings provide insights and directions for future agronomic management under global changes.

To obtain a deeper understanding of the seed quality variations to simulated N deposition, further analysis was conducted in the seed protein content in response to different classification factors including crop species, N deposition forms, and N deposition rates (Figure 5a and Figure S5a). This analysis demonstrated a consistent positive role of N deposition in seed protein content, a result of the well-accepted metabolic connections between the N element and protein synthesis (Gilbert et al., 2021; Scheible et al., 2004). Moreover, our GVA demonstrated an “excess synthesis” of seed protein content in response to simulated N deposition (Figure 6c), which again strongly supports the positive effects of N on seed protein content in oilseed crops. In this study, however, a contrasting finding emerged when considering the seed oil content response to global N deposition, which was not influenced by the different classification factors (Figures 1 and 5b). This result is consistent with a previous meta-analysis in soybean (Rotundo & Westgate, 2009), and our work widens the applicability of this physiological relationship to at least the whole family of oilseed crops, which also exhibit these adverse effects on a global scale. Strikingly, from the perspective of seed oil accumulation, a positive influence was observed (Figure S6). Therefore, the suppression of seed oil content could be partly attributed to the “dilution effect” caused by the increase in seed biomass on N deposition, which was further demonstrated by our GVA (Figure 6). In line with our hypothesis, previous studies have illustrated the presence of diluted plant nutrients or phenolic compounds due to increased biomass under N deposition (Sarwar et al., 2010; Sun et al., 2020). Equally, the antagonistic relationship between biomass and oil content could also be explained by the growth differentiation balance hypothesis (Le Bot et al., 2009; Peltonen-Sainio et al., 2011). According to this hypothesis, the differences in seed protein and oil content may be explained by an enhanced primary metabolism, including protein synthesis, and an inhibited secondary metabolism, including oil synthesis. Another possible reason might be that fatty acids do not require N for their synthesis (Tang et al., 2020). Therefore, the plant will tend to synthesize protein rather than fatty acid to consume excessive N (Rathke et al., 2005). Notably, fatty acids, the main components of oil, can act as key signaling compounds in responding to biotic and
abiotic stresses (Lim et al., 2017; Weber, 2002). Thus, it is possible that although fatty acid synthesis might be stimulated under N starvation conditions, it may be suppressed if sufficient N is sensed. Mechanistically, recent transcriptomic and metabolomic analysis in Arabidopsis thaliana and microalgae have demonstrated that N addition inhibits the activity of crucial enzymes or the expression of related genes involved in acyl lipid metabolism, changing the fatty acid components and reducing fatty acid content (Chu et al., 2019; Gaude et al., 2007; Janssen et al., 2020; Jouhet et al., 2017). These findings indicate that the seed’s inherent N status, as well as the seed biomass and protein content, together mediate the decreased oil content observed after simulated N deposition. These results suggest that the contradictory responses of seed protein and oil content to simulated N deposition may be balanced by both the changes in biomass changes and specific molecular regulatory pathways, suggesting directions for further investigation into the underlying mechanisms involved.

5 | CONCLUSIONS

This meta-analysis showed that simulated N deposition increases oilseed crop yield in a dose-dependent manner, and that this response was driven by crop species as well as the form of N deposition. Furthermore, the PNP, rather than other yield components, play vital roles in determining the yield response to simulated N deposition. This result suggests that the agronomic management of oil crops should consider the PNP response and that increasing the N input ratio during the vegetative period rather than the flowering stage would benefit the yields. The seed protein and oil contents, key indicators for evaluating seed quality, were affected differently by simulated N deposition, with a significantly increased protein content but decreased oil content. The changes in seed oil content may be determined by a biomass-induced dilution effect as well as biochemical and molecular pathways affected by N nutrition. In addition, the antagonistic relationship between protein and oil content should be considered in future oilseed crop planting. Specifically, when greater oil content is required in plants such as rape and sesame, the input of additional N should be reduced. In contrast, a good N supply is necessary for high protein contents in plants such as soybean. Overall, our meta-analysis assists in the prediction of oilseed crop responses to global N deposition, and therefore has significant ecological and agronomic value.

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CONFLICT OF INTEREST

The authors have declared that no conflict interests exist in this work.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Science Data Bank archive at https://doi.org/10.57760/sciedb.01765.

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