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Sulfur fertilization in soybean: A meta-analysis on yield and seed composition

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A R T I C L E I N F O

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A B S T R A C T

Sulfur (S) deficiency has been recently reported in soybean [*Glycine max* (L.) Merr.] producing regions across the United States. However, field studies have often failed to demonstrate a strong relationship between yield and S fertilization and generally attributing the lack of yield response to unfavorable weather and high soil S supply. In addition, only a few reports described seed composition changes due to S availability under contrasting field conditions. Therefore, our goals were (i) to implement a meta-analytic model to quantify the effect of S application at different growth stages on yield and seed concentration of protein, oil, essential non-S amino acids, and S amino acids (SAA, cysteine and methionine); ii) identify environmental factors underpinning the response of S to these plant traits. Field experiments were carried out from 2017 to 2019 growing seasons with a total of 44 unique site-years conditions across 18 locations in 8 states. Mineral S fertilizer (sulfate/ elemental S) was supplied depending on the study at sowing, vegetative and/or reproductive stages. A random-effects multilevel meta-analysis was conducted. The effect sizes compared yield and seed composition responses relative to the unfertilized control. A principal component analysis (PCA) separated distinctive environmental conditions and a sub-grouped meta-analysis with the main environmental factors was later executed to understand the response of the plant traits with those factors. Seed protein concentration increased by 0.3 % when S was applied at sowing. The concentration of SAA increased by ca. 1% regardless of the fertilization timing. Sites exposed to drought stress (18–29% reduction of potential transpiration) neither presented changes in yield nor seed composition due to S fertilization. Soils with organic matter between 25 and 32 g kg^{-1} (medium cluster) displayed significant responses to S application. This research brings extensive data and provides a comprehensive analysis of weather and soil attributes influencing soybean yield and seed composition responses to S availability.

Abbreviations: AMS, ammonia sulfate; ET, evapotranspiration; MES, micro essentials S10®; N, Nitrogen; PDC, principal components analysis; RS, reproductive sulfur; S, Sulfur; SAA, Sulfur amino acid; SOM, Soil organic matter; SS, sowing sulfur; T_{pot}, Potential transpiration; T_{red}, Transpiration Reduction; T_{act}, Actual transpiration; VS, vegetative sulfur.

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1. Introduction

Soybean [*Glycine max* (L.) Merr.] is the front-runner crop for plant-based protein production accounting for 70 % of global meal consumption (USDA, 2020). The high seed protein concentration is valuable for animal feeding due to the low cost of production and a relatively complete amino acid profile (Cromwell, 2008; Medic et al., 2014). However, soybean meal has low sulfur amino acid (SAA) concentration relative to other AA and often needs to be enriched with exogenous methionine and cysteine, particularly for feeding monogastric livestock (Krishnan, 2015; Parsons, 1996). Efforts have been made to select for varieties (inbred lines) with high concentration of SAA (methionine and cysteine) in soybean seeds (Krishnan and Jez, 2018; Wilcox and Shibles, 2001). However, the synthesis of SAA is linked to quantitative traits and therefore prone to environmental influence (Krishnan and Jez, 2018; Panthee et al., 2006). Nevertheless, low sulfur (S) availability in major soybean-producing regions has been reported worldwide (Ceccotti et al., 1998; Pias et al., 2019; Scherer, 2001). Thus, improving S supply may lead to higher S-containing proteins than seeds produced using current management practices (without S application).

Sulfur availability and assimilation by soybean are closely related to SAAs expression in vegetative and reproductive organs (Hitsuda et al., 2015; Marschner, 2011), impacting both concentration (Hitsuda et al., 2004) and quality of seed storage proteins (Sexton et al., 1998a). The SAAs constitute 80 % of all plant organic S (Anderson, 1990). Thus, it would be expected that an increase of SAAs follow an rise in S assimilation. Indeed, seed S concentration is associated to protein concentration with a constant N:S ratio (Wilcox and Shibles, 2001). In field conditions, Kaiser and Kim (2013) reported an increase of 2.1 % in seed protein in 2 out of 3 experiments due to S fertilization without specifying the type of storage protein. The main reserve proteins in soybean embryos are the low S content conglycinin and high S content glycinin (also known as 7S and 11S, respectively), which together constitute 70 % of seed protein (Hitsuda et al., 2015; Koshiyama, 1983) and present. However, 7S is considered poor-quality protein due its low SAA content. The 11S is favored by sufficient S supply, whereas 7S is favored in N rich media (Sexton et al., 1998a) via a compensatory balance regardless of seed protein concentration (Yang et al., 2016). Despite evidence of relationship between S nutrition and soybean seed composition, little is known about the interaction with environmental conditions, and how to translate S management into improved nutritional quality.

The development stage in which S deficiency occurs affects the expression of quality traits in the seed. Sulfur is considered to have a low mobility in plants (Marschner, 2011) and S mobilization from vegetative to reproductive plant tissue is less efficient than N (Sexton et al., 2002). Although soybean accumulates high amounts of SAA in leaves during vegetative development, this S reservoir is unavailable to meet late reproductive requirements (Sunarpi and Anderson, 1996a, 1996b). Naeve and Shibles (2005) found mobilized S to be essential for seed SAA accrual and that S acquired by the plant later in development was more efficiently mobilized to the seed. The seed 11S concentration is relatively unresponsive to S availability during vegetative but is reduced by S-deficiency during reproductive stages (Sexton et al., 1998a). These observations suggest that a S management strategy for improving seed quality must assure sufficient S until late plant development. From the seed yield perspective, in-season assessment of the S status for supporting fertilizer recommendation have been proposed (Divito et al., 2016). However, no research has been done at the field level to validate the effect of S top-dressing fertilization during late vegetative or reproductive stages on seed quality.

Conversely, the relationship between yield and S fertilization before or at sowing is more commonly reported in field experiments. However, results are erratic, and S deficiency negatively impacting yield is not often documented (Gutierrez Boem et al., 2007; Hitsuda et al., 2015). Usually, S fertilization responses are linked to N nutritional status (Abdin et al., 2003; Gutierrez Boem et al., 2007). Kaiser and Kim (2013) reported soybean yield responses in only one out of three sites, linking the lack of yield response to S due to the high level of soil organic matter. Divito et al. (2015) documented a positive soybean yield response to S in nine out of 15 sites, attributing the response to low levels of soil S due to an intensive crop rotation. Different yield potentials were related to soybean yield responses reported in 11 out of 20 field trials across Argentina (Salvagiotti et al., 2012). Casteel et al. (2019) demonstrated yield responses to S application in soils with low soil organic matter. Based on these divergent findings, it is evident current information is insufficient to shade light onto the interactions between soil nutrient status, weather, and fertilizer application timing within a large array of geographical environments.

To provide a robust inference across a range of geographical environments, a meta-analysis is a statistical method quantitatively integrating a large collection of individual studies. It is commonly used in conjunction with systematic review of available published data in order to draw a 'review generated evidence' over a collection of results (Borenstein et al., 2011; Madden and Paul, 2011). However, performing the meta-analytic process over raw data of multiple experiments is often referred as individual participant data (IPD) meta-analysis (Stewart and Tierney, 2002; Yellareddygari et al., 2016). The IPD is advantageous over traditional meta-analysis for not presenting publication bias (Easterbrook et al., 1991; Riley, et al., 2010; Stewart and Tierney, 2002). Finally, meta-analyses are useful since they do not rely on a unique experimental design across different trials (Riley, et al., 2010). Thus, the utilization meta-analysis method was pursued with the goal of: i) quantifying the effect of S application at different timing on yield, seed protein concentration, oil, essential non-S amino acids, and SAA, and ii) identifying the main environmental variables underpinning the response of seed yield and quality to S application.

2. Material and methods

2.1. Experimental design and treatments

Soybean field studies were carried out across eight states of the US Midwest and South (Arkansas, Illinois, Indiana, Kansas, Kentucky, Minnesota, North Dakota, and South Dakota), from the 2017 to 2019 growing seasons. The dataset comprises 72 individual studies with a unique combination of location, year, sowing date, and genotype (Table 1). Studies sharing the same geolocation growing season accounted for 44 unique site-years conditions across 18 locations. Each individual study presented an unfertilized control treatment and S fertilization treatment during at least one of the following developmental phases: at sowing (SS), vegetative (VS), and reproductive (RS). A total of 114 individual participant data (effect sizes) were used in the meta-analysis. The standard S fertilization in the abovementioned regions is one time-application of S from 0 to 25 kg ha^{-1} pre- or at sowing (Leikam et al., 2003; Sawyer et al., 2015).

The SS fertilization was performed within 10 days before or during sowing. The VS top dressing fertilization ranged from the fourth trifoliolate (V4) to the eighth trifoliolate (V8) growth stages, whereas the RS top dressing ranged from flowering (R1) to beginning of seed filling (R5) growth stages (Fehr et al., 1971). The main S sources were either Micro essentials S10® (MES - Mosaic, Tampa, FL) (monoammonium phosphate with ammonium sulfate and sulfur 12-40−00 + 10, N-P-K + S), pure ammonium sulfate (21-00-−00 + 24) or magnesium sulfate (14 % of S). The S rates ranged from 9 to 22 kg ha^{-1}. Each study comprised three to five replications in a randomized complete block design. Since some of the fertilizer sources also contained other nutrients, mainly P (from 0 to 22 kg ha^{-1}) and N (from 0 to 45 kg ha^{-1}), an exploratory analysis was executed using these elements as moderators, and concluding that those factors did not present significant impact either on yield or on seed composition traits (data not shown). Nevertheless, crop response was not expected to these doses of P (Leikam et al., 2003; Sawyer et al., 2015) and N (Mourtzinis et al., 2018) in our field conditions.

Table 1
Overall experimental characteristics for 72 unique combination studies used in the meta-analysis.

State	City	Year	Sowing date	Genotype	Timing of application [a]	Sulfur Rate (kg ha^{-1})	Sulfur Source [b]	Soil group
AR	Fayetteville	2018	18-May	P41T33R	RS	9	AMS	Fragiudults
AR	Fayetteville	2018	18-May	P46T59R	RS	9	AMS	Fragiudults
AR	Fayetteville	2018	14-Jun	P41T33R	RS	9	AMS	Fragiudults
AR	Fayetteville	2018	14-Jun	P46T59R	RS	9	AMS	Fragiudults
AR	Fayetteville	2019	11-Jun	P41T33R	RS	9	AMS	Fragiudults
AR	Fayetteville	2019	11-Jun	P46T59R	RS	9	AMS	Fragiudults
AR	Fayetteville	2019	27-Jun	P41T33R	RS	9	AMS	Fragiudults
AR	Fayetteville	2019	27-Jun	P46T59R	RS	9	AMS	Fragiudults
AR	Fayetteville	2019	11-Jun	P45A29L	SS	9	AMS	Fragiudults
AR	Pine Tree	2019	15-Jun	P42A96X	RS	9	AMS	Fraglossudalfs
AR	Pine Tree	2019	15-Jun	P45A29L	RS	9	AMS	Fraglossudalfs
IL	Champaign	2018	16-May	AG34 × 6	SS	22	MES10	Argiudolls
IL	Champaign	2018	16-May	GH3546X	SS	22	MES10	Argiudolls
IL	Ewing	2019	11-Jun	AG34 × 6	SS	22	AMS /MES 10	Hapludalfs
IL	Ewing	2019	11-Jun	GH3546X	SS	22	AMS /MES 10	Hapludalfs
IL	Harrisburg	2017	10-May	AG4135	SS	22	MES10	Argiudolls
IL	Harrisburg	2017	10-May	GH3546X	SS	22	MES10	Argiudolls
IL	Harrisburg	2017	10-May	GH4142X	SS	22	MES10	Argiudolls
IL	Harrisburg	2017	10-May	R2C4000	SS	22	MES10	Argiudolls
IL	Harrisburg	2017	10-May	Rx3556	SS	22	MES10	Argiudolls
IL	Harrisburg	2018	2-May	AG34 × 6	SS	22	MES10	Argiudolls
IL	Harrisburg	2018	2-May	GH3546X	SS	22	MES10	Argiudolls
IL	Savoy	2019	3-Jun	AG34 × 9	SS	22	AMS /MES 10	Argiudolls
IL	Savoy	2019	3-Jun	AG34 × 6	SS	22	AMS /MES 10	Argiudolls
IL	Savoy	2019	3-Jun	GH3546X	SS	22	AMS /MES 10	Argiudolls
IL	Yorkville	2018	19-May	AG34 × 6	SS	22	MES10	Endoaquolls
IL	Yorkville	2018	19-May	GH3546X	SS	22	MES10	Endoaquolls
IL	Yorkville	2019	10-Jun	AG34 × 6	SS	22	MES10	Endoaquolls
IL	Yorkville	2019	10-Jun	GH3546X	SS	22	MES10	Endoaquolls
IN	Wanatah	2018	25-May	AG24 × 7	SS / VS / RS	11	AMS	Argiaquolls
IN	Wanatah	2018	25-May	AG34 × 6	SS / VS / RS	11	AMS	Argiaquolls
IN	Wanatah	2019	4-Jun	AG24 × 7	SS / VS / RS	11	AMS	Argiaquolls
IN	Wanatah	2019	4-Jun	AG34 × 6	SS / VS / RS	11	AMS	Argiaquolls
IN	Wanatah	2019	7-Jun	AG24 × 7	SS	11	AMS	Argiaquolls
IN	Wanatah	2019	7-Jun	AG24 × 7	SS	11	AMS	Argiaquolls
IN	Wanatah	2019	7-Jun	AG34 × 6	SS	11	AMS	Argiaquolls
IN	West Lafayette	2018	11-May	AG34 × 6	SS / VS / RS	11	AMS	Endoaquolls
IN	West Lafayette	2018	5-Jun	AG34 × 6	SS / VS / RS	11	AMS	Endoaquolls
IN	West Lafayette	2018	24-May	AG24 × 7	SS	11	AMS	Endoaquolls
IN	West Lafayette	2018	24-May	AG34 × 6	SS	11	AMS	Endoaquolls
IN	West Lafayette	2019	11-Jun	AG34 × 6	SS / VS / RS	11	AMS	Endoaquolls
IN	West Lafayette	2019	27-Jun	AG34 × 6	SS / VS / RS	11	AMS	Endoaquolls
IN	West Lafayette	2019	12-Jun	AG34 × 6	SS	11	AMS	Endoaquolls
IN	West Lafayette	2019	12-Jun	AG24 × 7	SS	11	AMS	Endoaquolls
IN	West Lafayette	2019	12-Jun	AG34 × 6	SS	11	AMS	Endoaquolls
KS	Manhattan	2019	5-Jun	AG39 × 7	SS	22	AMS	Udifluvents
KS	Rossvile	2019	31-May	P34T43R2	RS	22	$MgSO_4$	Hapludolls
KS	Rossvile	2019	31-May	P39T67R	RS	22	$MgSO_4$	Hapludolls
KS	Topeka	2018	10-May	P34T43R2	RS	22	$MgSO_4$	Hapludolls
KS	Topeka	2018	10-May	P39T67R	RS	22	$MgSO_4$	Hapludolls
KS	Topeka	2019	15-May	AG39 × 7	SS	22	$MgSO_4$	Hapludolls
KY	Princeton	2019	14-May	P46A57BX	SS	22	AMS	Paleudalfs
MN	Saint Paul	2018	11-May	AG14 × 7	RS	11	AMS	Hapludolls
MN	Saint Paul	2019	7-May	AG14 × 7	RS	11	AMS	Hapludolls
MN	Saint Paul	2019	7-May	AG14 × 7	SS	11	AMS	Hapludolls
ND	Prosper	2019	31-May	AG06 × 8	SS	11	AMS	Calciaquolls
SD	Beresford	2017	9-May	P22T73	SS / RS	11	AMS	Haplustolls
SD	Beresford	2018	17-May	AG11 × 8	SS / VS / RS	11	AMS	Haplustolls
SD	Beresford	2018	17-May	AG24 × 7	SS / VS / RS	11	AMS	Haplustolls
SD	Beresford	2019	8-Jun	AG11 × 8	SS / VS / RS	11	AMS	Haplustolls
SD	Beresford	2019	8-Jun	AG24 × 7	SS / VS / RS	11	AMS	Haplustolls
SD	Beresford	2019	8-Jun	AG24 × 7	SS	22	AMS	Haplustolls
SD	Brookings	2017	31-May	P15T46	SS / RS	11	AMS	Haplustolls
SD	Brookings	2018	15-May	AG11 × 8	SS / VS / RS	11	AMS	Haplustolls
SD	Brookings	2018	15-May	AG24 × 7	SS / VS / RS	11	AMS	Haplustolls
SD	Brookings	2018	4-Jun	AG11 × 8	SS / VS / RS	11	AMS	Haplustolls
SD	Brookings	2018	4-Jun	AG24 × 7	SS / VS / RS	11	AMS	Haplustolls
SD	Brookings	2019	3-Jun	AG11 × 8	SS / VS / RS	11	AMS	Haplustolls
SD	Brookings	2019	3-Jun	AG24 × 7	SS / VS / RS	11	AMS	Haplustolls
SD	Brookings	2019	13-Jun	AG11 × 8	SS / VS / RS	11	AMS	Haplustolls
SD	Brookings	2019	13-Jun	AG24 × 7	SS / VS / RS	11	AMS	Haplustolls
SD	Brookings	2019	3-Jun	AG24 × 7	SS	22	AMS	Haplustolls

[a] SS: sowing S fertilization; VS: vegetative S fertilization; RS: reproductive S fertilization.
[b] AMS: Ammonium sulfate (21—0—0—24S); MES10: Microessentials-S10® (12—40—0—10S); $MgSO_4$: Magnesium sulfate (14 % of S).

2.2. Plant measurements and environmental data

Seed yield was obtained from each experimental unit by combine harvesting the plot central rows and adjusting seed moisture to 130 g kg^{-1} of water content. From the harvester auger, a seed sample of about 0.5 kg was collected, and later ground to 0.1 mm particle size. Seed protein, oil, and amino acid concentrations were all obtained using near-infrared spectroscopy using a Perten DA7250 Feed Analyzer (Perten Instruments, Stockholm, Sweden) calibrated based on the AOAC 982.30 (AOAC, 2016). The calibration is based on the regression from Honigs (1985) and the retrieved cross-validation R^2 values for all 18 amino acids ranged from 0.56 to 0.89. More specifically, the R^2 values for cysteine and methionine were of 0.58 and 0.56, respectively. This method estimates the concentration of the seed components in dry basis. The concentration of the 10 essential amino acids was compiled for two groups: 1) the SAAs, cysteine and methionine; and 2) the eight essential non-S containing amino acids: lysine, threonine, tryptophan, isoleucine, leucine, histidine, phenylalanine, and valine.

Sites were characterized in terms of soil extractable S concentration [monocalcium phosphate extraction (Combs et al., 1998)] and soil organic matter [SOM; acid digestion (Combs and Nathan, 1998)] before the onset of each study. Based on latitude and longitude coordinates, weather data were retrieved from the Google Earth Engine platform (Huntington et al., 2017). The average growing season value of air temperature, humidity, vapor pressure deficit (VPD), drought stress, and the sum of rainfall precipitation, reference evapotranspiration (ET_0) and solar radiation were used as weather descriptors. The Polaris database was used to acquire the soil texture from 0 to 0.15 m depth with 30 m pixel resolution (Chaney et al., 2016). Since a single location could host more than one study, a unique combination of weather and soil data resulted in 44 experimental conditions (different coordinates and non-overlapping growing seasons). The overall characteristics of these locations are presented in Table 1.

2.3. Drought stress

The crop evapotranspiration and water extraction from soil were estimated using Soil, Water, Atmosphere and Plant model (SWAP) (Kroes et al., 2008). The SWAP model simulates water transport in the vadose zone integrating Richards' equation to Mualem-Van Genuchten relation and Wofost crop model. The upper limit condition was defined by the Penman-Monteith ET_0 (Allen, 1998). Crop potential evapotranspiration (ET_c) was calculated using simulated crop coefficient and modifying Penman-Monteith ET_0 (Bouman et al., 2001). The parameters for the water retention curve (ksat, θ_{sat}, θ_{res}, *m,* and α) were also extracted from the Polaris database from 0.05 to 0.6 m depth (Chaney et al., 2016). To minimize the effect of initial soil moisture, the simulations were begun on January 1st, at least four months before sowing. The crop initialization began at the reported planting dates and the cycle length was defined by maturity group of each genotype in the WOFOST detailed model (Boons-Prins et al., 1993). Drought stress was given by the reduction in crop transpiration when soil water potential decreased bellow −80 kPa in low ET potential or −50 kPa in high ET potential (Clemente et al., 1994; Feddes et al., 2001). Drought stress is the percentual of transpiration reduction (T_{red}) given by Eq. 01.

$$T_{red} = \left(\frac{T_{Pot} - T_{Act}}{T_{Pot}}\right) x\,100 \qquad (01)$$

Where T_{pot} is the simulated potential transpiration and T_{act} is the simulated actual transpiration. It ranges from 100 % to 0%, where 100 % is severe transpiration reduction (severe drought stress) and 0% indicates the actual transpiration was equivalent to the potential (no drought stress).

2.4. Meta-analysis moderators

The timing of S fertilization (SS, VS, and RS) was part of the research question and was selected as moderator in the first grouped meta-analysis. Posteriorly, the available weather (average air temperature, humidity, drought stress, VPD and total rainfall precipitation, radiation, ET_0 in the season) and soil (SOM, S concentration, clay) covariates were subjected to a principal component analysis (PCA) using R software with the "Factoextra" package (Kassambara and Mundt, 2020; R Core Team, 2019). The main goal of the PCA was to identify variables that explained most of the environmental variability and find non-correlated factors for the grouped meta-analytic models. The retention criterion of eigenvalue greater than one was used to define the number of dimensions. We selected weakly correlated environmental factors with a great contribution in each dimension. The chosen variables were subjected to cluster analysis using the k-means model (Chinrungrueng and Sequin, 1995) and classified as low, intermediate, or high levels for a straightforward interpretation.

2.5. Meta-analysis models

A one-step meta-analysis was performed modeling all data simultaneously while accounting for the clustering of participants within studies. (Riley et al., 2010).The effect sizes were derived from the percentual response of the treatment with S fertilization (at different timings) over the unfertilized control using the "*metaphor package* in R" (Viechtbauer, 2010). Considering the control treatment was shared among studies with multiple fertilization timings, a multilevel model was adopted. In this case, not only the between study variance is assumed, but also another layer of error structure (accounting for the shared control treatment). Different meta-analytic models were fitted for each response variable, considering a model without moderators, for estimating the overall summary of effect sizes, and models for each one of the moderators, with the sub-groups: low, intermediate, and high. The heterogeneity statistics (I^2), representing the proportion of the unexplained between-study variance, was estimated for each model. The lower the I^2 the better the moderator subgroups separated responses to S fertilization. Variance, and consequently weight, was known for all the studies, and since data came from field trials, the risk for publication bias is very low and thus not considered in the analysis (Ahmed et al., 2012).

3. Results

There was a large geographical dispersion of all studies across the US soybean producing region for three growing seasons (2017, 2018, and 2019), encompassing from the latitudes from 35.12 °N to 47.00 °N and longitudes from 86.90 °W to 97.10 °W (Fig. 1). Average temperature and precipitation were compared to the 30-years climate normal (1981–2010) for each site. A greater amplitude and deviation were observed in rainfall than in the average seasonal temperature. Only 9 site-years recorded dryer years than the 30-years normal, with 35 site-years with greater precipitation. Over 30 % rainfall variations was observed even within the same state but between growing seasons (IL, AR, KS, IN). A total of 27 out of 44 site-years presented warmer and wetter year than the historical normal and none of the evaluated sites were classified as cold and dry.

3.1. Overall effect size and time of S fertilization

The overall effect sizes of S application on yield, seed protein, SAAs, and oil concentrations were significant. Yield increased by 1.6 %, seed protein concentration by 0.3 %, and SAA by 1%, whereas oil decreased by 0.3 %, whereas for essential non-Samino acids this effect was not significant (Fig. 2). However, grouping the studies by the timing of application provided different effects sizes when S was supplied at

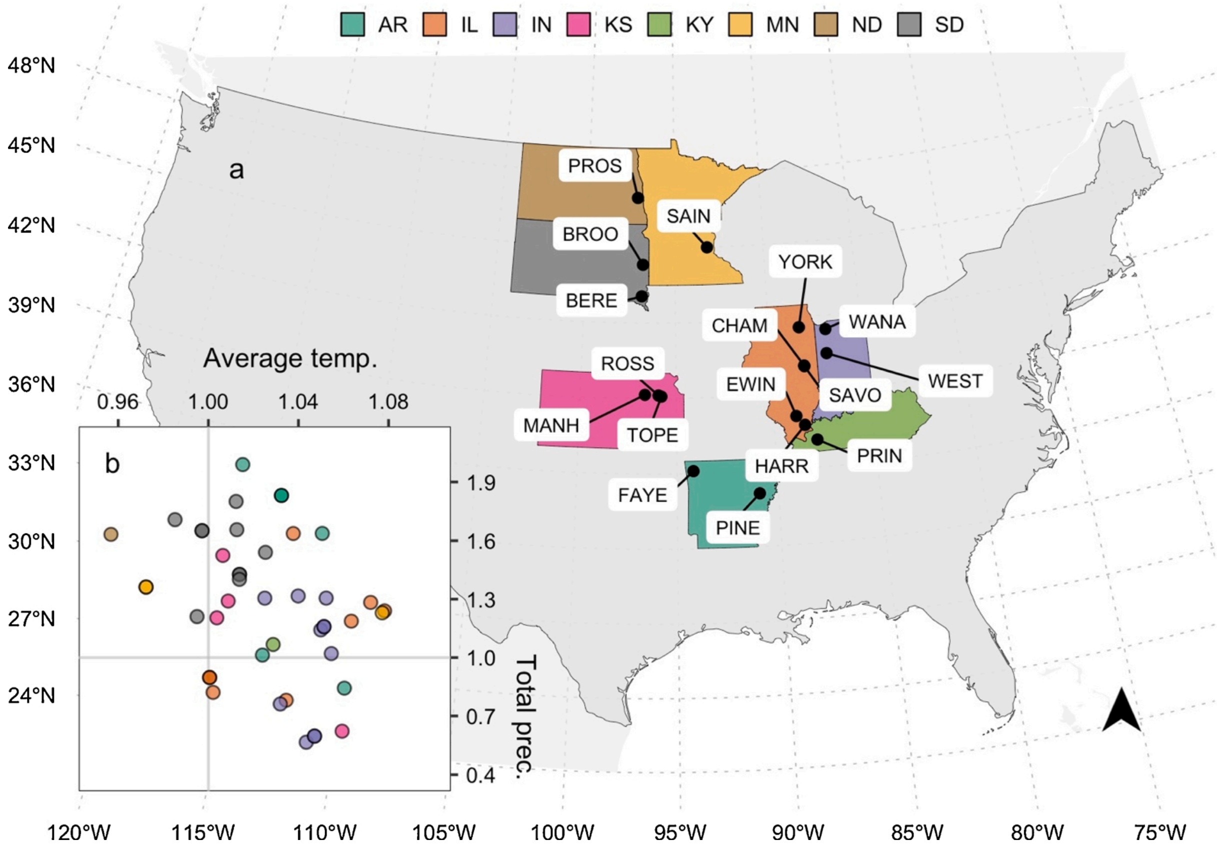

Fig. 1. States and cities (in proximity to the experimental site) where studies were performed in at least one of the three growing seasons (2017, 2018, and 2019) (a). Each location comprehends at least one comparison between unfertilized control versus sulfur application. The insert panel (b) is the contrast between the seasonal average temperature (average temp.) and rainfall precipitation (total prec.) with the 30-year climate normal (1981-2010) (gray lines).

sowing, vegetative, or reproductive stages. All evaluated traits were significantly affected only due to the application of S at sowing (SS), with an increase of 1.7 % for yield, 0.4 % for seed protein, and 0.3 % for essential non-S amino acids, and a decrease of 0.3 % for oil (Fig. 2). Unlike other measures, the SAA concentration was positively affected regardless of the timing of the S application. The increase of SAA concentrations on the S fertilized group was 1.0 %, 1.0 % and 1.1 % for SS, VS, and RS fertilization timing, respectively. The overall meta-analysis, or even when grouped by the timing of application, had a relatively high level of inconsistency across studies (I^2). The heterogeneity ranged from 42.3 % (oil) to 82.2 % (SAA) in the overall model and from 41.5 % (oil) to 82.4 % (SAA) when grouped by timing of fertilization. These inconsistency levels indicate a wide variation of the effect sizes among studies. A further sub-group meta-analysis with three levels of the most contrasting environmental factors was proposed to account for a large proportion of the variation in the evaluated traits and for potentially decrease the I^2, if those factors could become better moderators in the responses to S fertilization across site-years.

3.2. Environmental descriptors

Associations among environmental attributes (average air temperature, average air humidity, average VPD, average drought stress, total rainfall precipitation, total radiation, soil organic matter, soil S concentration, total ET_0) were explored via PCA. The two first principal components and the loadings to the fourth dimensions with an eigenvalue greater than one are shown in Fig. 3. The first component accounted for an overall variation of 40 % across studies. The higher loads on the first dimension were air temperature (22 %), VPD (20 %), and air humidity (19 %). The second principal component accounted for 22 % of the variation, mainly due to SOM (25 %), soil clay (22 %), drought (21 %), and precipitation (20 %). ET_0 (35 %) and radiation (33 %) accounted for most of the variance in the third dimension, whereas soil S presented a high load (89 %) in the fourth dimension (Fig. 3b). Data points from the same state showed similarities, with most of them placing together (Fig. 3a). The direction and length of the vectors in the bi-plot illustrate the ordination analysis results and variable correlations (Fig. 3a). Temperature, humidity, and VPD were positively correlated with variance explained most by temperature (Fig. 3). Both SOM and clay were also connected, with SOM having a strong contribution to the overall variance. Drought, radiation and ET_0 were positively correlated to each other and negatively associated with precipitation with drought stress depicting greater contribution to variance. Finally, the soil S concentration was poorly associated with the other environmental attributes and less varied among studies. The PCA reinforces the idea of the studies presenting a wide range of environmental conditions and supports the choice of some moderators to the following subgroup meta-analysis.

The average air temperature, SOM, drought stress, and soil S concentration were selected as moderators due to their significant contributions to the total variance, importance in their respective dimensions, and the absence of correlation supported by PCA. All the moderators were clustered in low, intermediate, and high levels according to the k-means model (Table 2). The drought stress ranged from 0% (no stress) to 4% in the low cluster, from 7 to 17 % in the intermediate cluster, and from 18 % to 29 % in the high cluster. Soil S concentration had a larger number of observations in the intermediate level (from 6.8–13.8 mg dm^{-3}). The SOM factor averaged 12 g kg^{-1} in the low cluster, 29 g kg^{-1} in the intermediate, and 38 g kg^{-1} in the high cluster (Table 2).

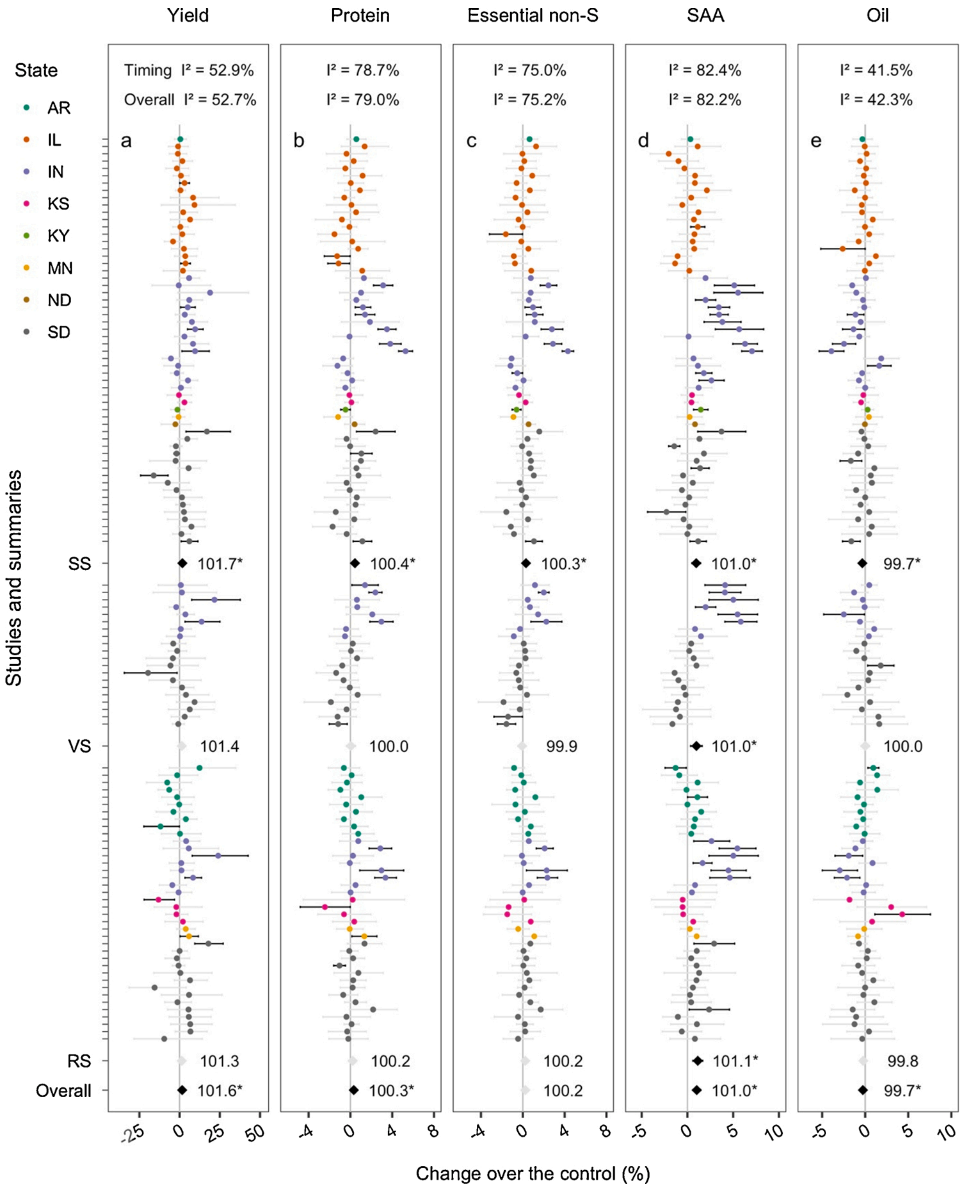

Fig. 2. Overall summary of effect sizes and the comparison between fertilized treatment and unfertilized control for each study grouped by the timing of application. Observed variables are seed yield (a), seed concentration of protein (b), essential non-S amino acids (c), sulfur amino acids (d), oil (e). SS, VS, and RS groups indicate sulfur application at sowing, vegetative, and reproductive stages, respectively. Black diamonds denote significant (*p-value*≤*0.05*) effect sizes, whereas gray diamonds denote non-significant (*p-value*>*0.05*) effect sizes between fertilized treatments and control. Circles represent point estimates and whiskers length their respective 95 % CI. Whiskers color denote whether the CI is covering zero (non-significant, gray) or not (significant, black). Summaries are followed by the I^2 = I-square statistic (%).

3.3. Grouped meta-analysis

Under high drought stress cluster, none of the evaluated response ratios for our plant traits were significant (Fig. 4). Yield was increased by S application in the intermediate and low drought environments by 4.1 and 1.6 %, respectively. Responses in seed protein and essential non-S amino acids were also observed in the intermediate drought cluster but not at the high and low drought clusters. Sulfur application increased SAA by 0.7 % in the low drought cluster and 2.0 % in the intermediate drought cluster. The level of inconsistency (I^2) when studies were grouped by drought stress was smaller for crop yield (46.1 %) than the overall heterogeneity reported in the first analysis (Fig. 2). The soil S concentration was a poor moderator for the yield response increasing the heterogeneity (I^2) for the effects on yield (53.5 % versus 52.7 % in the overall model) but decreasing the I^2 for the rest of the evaluated factors when compared to overall effect size. Only in the soils classified as intermediate S level, there were significant responses to the evaluated traits.

The level of SOM also was an important factor in determining the yield and seed quality responses to S application. Only when S was applied to the intermediate SOM cluster (from 25 to 32 g kg^{-1}), increases in yield (1.9 %), seed protein (0.7 %), and essential non-S amino acids (0.5 %) were observed (Table 2 and Fig. 4). Seed SAA was increased by S fertilization in soils with high (1.3 %) or intermediate (1.2 %), SOM levels, whereas seed oil concentration decreased by 0.5 % when S was applied to soils with intermediate SOM levels. The heterogeneity was estimated at 49.7 % for seed yield and 81.4 % for SAA when the response to S fertilization was classified by SOM clusters. Similarly, only the intermediate average air temperature significantly affected the response to S fertilization for yield (by 2.8 %), seed protein (by 0.8 %), seed essential non-S amino acids (by 0.6 %), seed oil (by 0.09 %) as well as seed SAA (by 2.1 %), reducing analysis heterogeneity only to seed yield (from 52.7 % to 52.2 %) and SAA (from 82.2 to % to 78.7 %).

4. Discussion

The meta-analysis has shown evidence on the effects of S supply on soybean yield and seed composition on a comprehensive dataset from field studies in a large range of environmental conditions in the US. More recently, attempts to correlate S application with yield (Casteel et al., 2019; Gutierrez Boem et al., 2007; Kaiser and Kim, 2013; Moreira et al., 2020; Salvagiotti et al., 2012) and seed composition (Bosaz et al.,

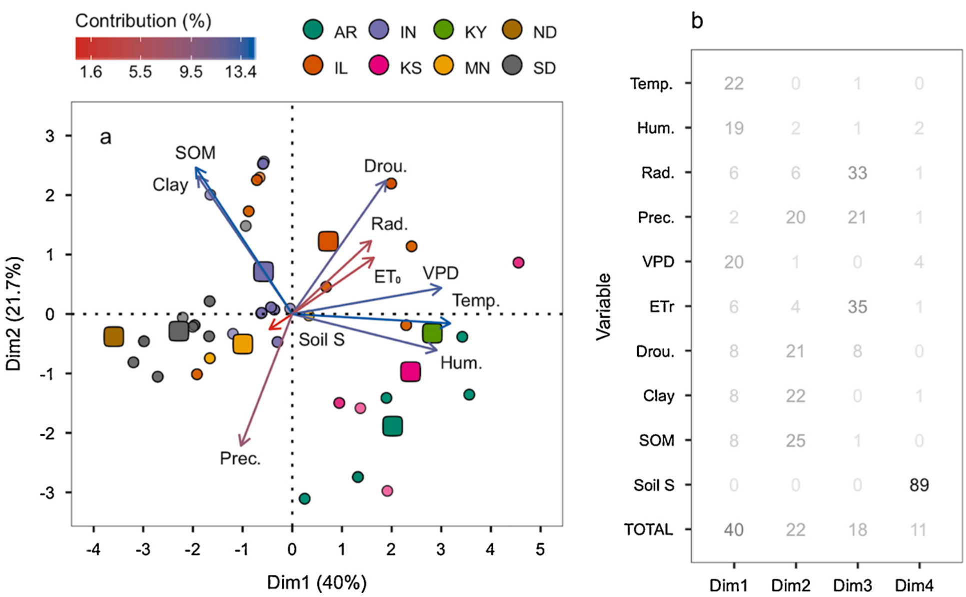

Fig. 3. Principal component analysis (PCA) of environmental factors across studies. Observation colors indicate the site-years grouped by state. Small circles are the individual locations, and squares are the group centroids. Factors are soil organic matter (SOM), sulfur concentration (Soil S), clay, total radiation (Rad.), total season reference evapotranspiration (ET_0), total season rainfall precipitation (Prec.), average vapor pressure deficit (VPD), average air temperature (Temp.), average humidity (Hum.), and average drought stress (Drou.). Vector colors shows the variable contribution magnitude (a). The respective contributions of each factor for total variance in the dimensions 1 to 5 (b).

Table 2
The average, minimum, maximum and number of observations for the clusters of environmental and agronomic moderators. Clusters boundaries were defined by K-means algorithm.

	Drought stress (% $T_{reduction}$)	Soil S concentration (mg dm^{-3})	Soil organic matter (g kg^{-1})	Temperature (°C)
Low	(*n* = *35*) 1 [0, 4]	(*n* = *21*) 3.7 [0.9, 6.0]	(*n* = *20*) 12 [5, 15]	(*n* = *16*) 17.4 v[14.8, 18.7]
Intermediate	(*n* = *20*) 12 [7, 17]	(*n* = *44*) 9.1 [6.8, 13.8]	(*n* = *42*) 29 [25, 32]	(*n* = *25*) 20.1 [19.0, 21.4]
High	(*n* = *17*) 23 [18, 29]	(*n* = *7*) 23.1 [17.0, 42.5]	(*n* = *10*) 38 [36, 40]	(*n* = *31*) 23.4 [21.9, 25.7]

[1] parenthesis n denotes the number of observations in each cluster.
[2] brackets values indicate the lowest and highest observations within a group.

2019; Fujiwara et al., 1992; Ham et al., 1975; Hitsuda et al., 2004; Islam et al., 2010; Sexton et al., 1998a) were pursued as well as to link the responses on seed components (e.g., oil, protein) to weather factors (Kumar et al., 2006; Pipolo et al., 2004; Rotundo and Westgate, 2009). However, to the extent of our knowledge this is one of the first studies linking yield and seed composition response to S fertilization with climatic and edaphic variables.

Implementation of a meta-analytic model is not a mechanistic approach to control all experimental effects (Marchionni and Reijula, 2019), however, it provides a strong association between the effect size and site conditions (Normand, 1999). Therefore, this quantitative analysis permitted us to summarize the effect of S fertilization across fertilization timings and different combinations of genotype, environment, and management conditions. The meta-analytic model adjusted to yield and seed components in this research portrayed high heterogeneity, even when expected in complex biological systems (Nakagawa et al., 2017). Nevertheless, yield and seed traits were positively impacted by S fertilization. Likewise, other authors demonstrated a similar effect of S on improving yield and seed composition, although not always consistently (Hitsuda et al., 2015; Kaiser and Kim, 2013; Salvagiotti et al., 2012). When S fertilization timing was introduced into the model, the heterogeneity slightly decreased for protein, essential non-Samino acids and oil, or even increased for yield and SAA, indicating that other factors better account for the yield and seed quality responses to S fertilization. Sulfur topdressing application during the vegetative and reproductive period has been found unlikely to improve seed yield, protein, or oil concentration, but has increased SAA in soybean seeds (Naeve and Shibles, 2005; Sexton et al., 1998b, 2002). Although the overall effects of S application presented here on yield and seed concentrations of protein, essential non-S amino acids, SAA, and oil were significant, the high heterogeneity must be considered as a limitation for a specific conclusion implying that S will improve yield and quality.

A lesson learned is that using environmental covariates helps us to reduce the heterogeneity and reveal the underlying factors that influence the yield and seed composition responses to S fertilization, as long as the sub-groups contain sufficient effect sizes for an unbiased conclusion. From a soil perspective, classifying results by different clusters of indigenous S and organic matter levels decreased heterogeneity (except for yield; Fig. 4). However, significant responses to S fertilization were observed only at the intermediate level of soil S and SOM. Many reports have shown the relationship of application of mineral S and crop performance, especially in low S environments (Hitsuda et al., 2004; Moreira et al., 2020; Zhao et al., 2008). Soil tests for predicting fertilizer responses to S in soybean are often considered as inaccurate, and other tools such as the N:S ratio in aboveground biomass (Divito et al., 2015; Salvagiotti et al., 2012) and seed (Hitsuda et al., 2004) have been proposed. Nevertheless, the narrow variance of soil S concentration across site-years (Fig. 3a) limits the power of the soil S sub-grouped model (Fig. 4). In contrast, SOM presented a greater variance across site-years but still presented relatively small effect sizes of participants in the lower SOM cluster. It might have contributed to the absence of a significant effect in the low level grouped model. Previous reports have associated a lack of response to S fertilization when SOM was above 34 g kg^{-1} (Kaiser and Kim, 2013). For the present study, yield responses to S fertilization were only observed with SOM levels ranging

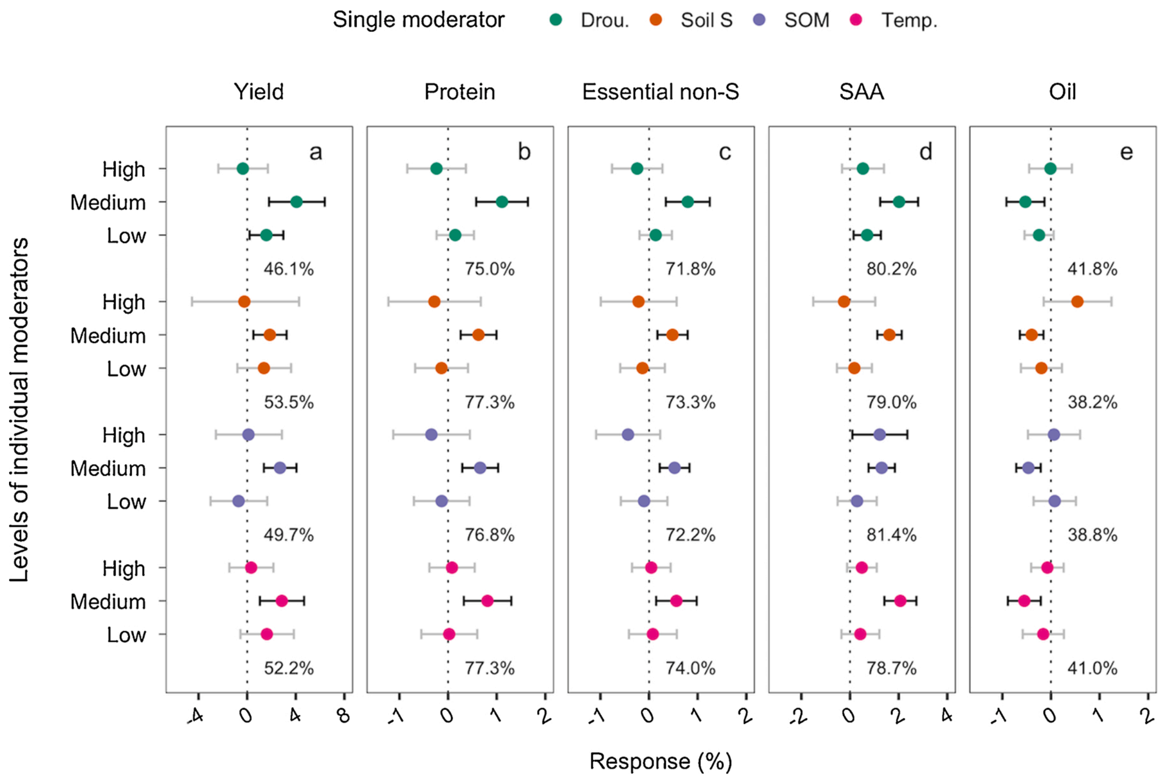

Fig. 4. Summary of effect sizes comparison between the S-fertilized versus unfertilized control, grouped by level of environmental and agronomic moderators: drought stress (green), soil sulfur concentration (orange), SOM (purple), and air average temperature (pink). Observed variables are seed yield (a), concentration of seed protein (b), essential non-S amino acids (c), sulfur amino acids(SAA) (d), and oil (e). Black diamonds denote significant (*p-value*$\leq$*0.05*) effect sizes, whereas gray diamonds denote non-significant (*p-value*>*0.05*) effect sizes between fertilized treatments and control. Circles represent point estimates and whiskers length their respective 95 % CI. Whiskers color denote whether the CI is covering zero (non-significant, gray) or not (significant, black). Summaries are followed by the I^2 = I-square statistic (%).

from 25 to 32 g kg^{-1}. Soil indigenous S supply depends on organic matter mineralization, N to carbon ratio, and S concentration (Bettany et al., 1980; Carciochi et al., 2018). Therefore, despite the significant relationship between soybean yield responses to S fertilization in combination with an intermediate level of soil organic matter, other factors seem to control the SOM mineralization and indigenous S availability.

When the model was grouped by drought level, it resulted in the lowest inconsistency across site-years for yield, seed protein and essential non-Samino acids. Decreased transpiration is result of stomatal closure, which also decreases carbon fixation and ultimately crop yield (Fàbregas and Fernie, 2019; Huck et al., 1983). Under such conditions, nutrient requirements decrease, and the crop becomes less responsive to mineral fertilization (Tanguilig et al., 1987). Our model did not account for the timing of drought stress and further studies are required to evaluate the effects of drought on S response at varying growth stages. In addition, temperature played a relevant role in reducing the heterogeneity observed in the SAA analysis. The correlation of air temperature to SAA concentration in seeds was reported by Wolf et al. (1982), noticing that a high temperature regime decreased cysteine synthesis but did not impairs methionine formation. In contrast, northern US locations were associated with lower concentration of SAA potentially connected to lower average T or radiation (Assefa, 2018). No prior research addressed how average air temperature throughout the season impacts SAA concentration in response to S fertilization, but the data presented here suggests an underlying relationship that deserves to be further investigated in future studies. In addition to drought stress and temperature, yield level as a final determinant reflected the effect of other potential stress factors. The combined effect of fertilizer N plus S in yield cannot be overlooked. Although the amount of N applied was relatively low compared to the total crop requirements (Bender et al., 2015), N fertilizer may impact yield under low nodulation conditions (Mourtzinis et al., 2018). The overall effect of S fertilization on seed protein concentration was in the same direction as the effect on yield. Seed protein concentration increased when S fertilizer was applied only at sowing (Fig. 2), possibly due to the combined effect of S improving biological N fixation (Zhao et al., 2008) or as a direct consequence of a starter N-fertilizer (Caliskan et al., 2008; Osborne and Riedell, 2006; Starling et al., 1998). However, the effects of the in-season S fertilization (VS and RS) impacting only SAA and not protein or essential non-S amino acids concentration are evidence of greater effect of S than N fertilization. The increment of N availability to the plant has been found to be negatively related to the SAA concentration (Sexton et al., 2002, 1998a). If the consequential N fertilization was notable, there would be expected an increase in the total seed protein (Rotundo and Westgate, 2009) instead of the increment in observed higher SAA concentration.

In summary, the data reported here showed strong evidence of S fertilization affecting soybean traits in regards to the timing of application. However, there still remained a relatively high level of uncertainty in the analyses due to the high amount of variability left unexplained by the model. Remarkably, the meta-analytic model did not account for genotype differences and information regarding S-response behavior in modern commercial varieties is scarce for contextualization with our results. Additional moderators could potentially decrease the model heterogeneity, such as genotype, crop rotation, atmospheric S deposition, or other factors that modulate the S supply. Nevertheless, further research to determine the effects of S application on yield and seed composition combined with more controlled environmental conditions will strengthen the associations presented in this study. Exploring the interaction between genotype and environment could better understand soybean responsiveness to S and identify genotypes with different nutrient use efficiencies. Lastly, expanding the geographical inference level and including more emphasis on screening potential responsive environments would enhance the understanding of the responses to changes in S supply.

5. Conclusion

A recurrent response in seed yield, protein, and methionine and cysteine concentrations to S application was identified in soybeans, and environmental conditions were associated with reducing heterogeneity in the meta-analysis. The introduction of S timing as a moderator (subclass) in the meta-analyses was able to group significant responses to S fertilization primarily at sowing time for most of the evaluated traits. In contrast, seed SAA level increased regardless of the S fertilization timing. Environments prone to drought stress (with low potential yield) were less likely to foster significant yield or seed quality changes in response to S fertilization. Application of S fertilizer is demonstrated here as a feasible crop management practice for improving seed quality via an increased concentration of cysteine and methionine. Future research should attempt to integrate S nutritional status throughout the cycle identifying critical S thresholds predicting high seed concentration of sulfur amino acids.

CRediT authorship contribution statement

Ignacio A. Ciampitti: secured funding, lead the project, conceptualized hypotheses, research questions, and developed the study design. **Ignacio A. Ciampitti, Péter Kovács, Larry C. Purcell, Frederick E. Below, Shaun N. Casteel, Carrie Knott, Hans Kandel, Seth L. Naeve, Sotirios Archontoulis:** provided leadership and/or execution of data collection. **Luiz H. Moro Rosso, André Fróes de Borja Reis:** developed the code for data analysis and visualization. **André Fróes de Borja Reis:** drafted the manuscript. **Ignacio A. Ciampitti, Walter Carciochi, Willian J. Ross, Vitor Rampazzo Favoretto, Dan Davidson, Péter Kovács, Larry C. Purcell, Frederick E. Below, Shaun N. Casteel, Carrie Knott, Hans Kandel, Seth L. Naeve, Luiz H. Moro Rosso:** made critical revision to the manuscript and contributed to the final version.

Additional information

The authors declare they have not any competing financial interests or personal relationships that could have influenced the research and this scientific communication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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