



Irrigation increases on-farm soybean yields in water-limited environments without a trade-off in seed protein concentration

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ABSTRACT

Context or problem: A trade-off between seed protein concentration (SPC) and yield has been reported for soybean. Therefore, assessing management practices that can nullify this trade-off is relevant to avoid further declines in SPC in the future as yield continues to increase. While the positive effect of irrigation on yield is well documented, only a few studies have assessed the impact of irrigation on SPC, showing conflicting results.

Objective or research question: The objective was to determine if the trade-off between seed yield and SPC persists when irrigation is applied and how management, soil, and weather factors influence the trade-off. We hypothesized that yield increases induced by irrigation would likely decrease SPC.

Methods: Our experimental approach involved the use of producer-reported data, *in-situ* seed collection, and crop modeling. Yield and management data were collected from 268 soybean fields in Nebraska (USA), along with data on SPC, seed oil concentration (SOC), and seed carbohydrate concentration (SCC) determined from samples collected in each field. Field-specific phenological data were derived from model simulations. The combined data were then used to assess the effect of irrigation on seed yield and constituents as influenced by management, soil, and weather factors.

Results: On average, both seed yield (+0.86 Mg ha⁻¹) and SPC (+3.2 g kg⁻¹) were higher, but SOC (-2.0 g kg⁻¹) was lower, and SCC was unaffected in irrigated *versus* rainfed field pairs. Yield and SPC increased simultaneously in response to irrigation in two-thirds of the fields, especially when environmental conditions did not favor seed oil synthesis (e.g., cooler temperature and less incident solar radiation). A trade-off of higher seed yield and lower SPC occurred with irrigation in the remaining fields wherein conditions were favorable for seed oil synthesis (e.g., warmer temperatures and greater radiation).

Conclusions: Despite higher seed yield generated in irrigated *versus* rainfed fields, no concurrent reduction occurred in SPC in the majority of irrigated fields – a surprising finding that was not consistent with the general expectation that higher soybean yields typically result in yield-SPC trade-off.

Implications or significance: This study showed that irrigation-induced higher soybean yields are possible without an attendant SPC penalty when temperatures and radiation are conducive for its mitigation. We are unaware of any other yield-increasing practices – except nitrogen (N) fertilization – that do not result in a concomitant decline in SPC. A hypothesized higher N supply *via* soil N mineralization and/or biological N fixation in irrigated fields in this study may explain the absence of yield-protein trade-off.

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1. Introduction

Soybean is the main source of vegetable protein in the world (FAO-STAT, 2023; Medic et al., 2014). One kilogram of soybean seed contains ca. 340 g protein, 190 g oil, 290 g carbohydrate, and 50 g minerals on a 130 g kg⁻¹ seed moisture content (Medic et al., 2014). Seeds are usually processed to extract oil, and the remaining meal fraction is mostly used as a protein source for animal feed (Grassini et al., 2021; Medic et al., 2014). A recent study showed that seed protein concentration (SPC) in the U.S. decreased from 1986 to 2021 at a rate of 0.49 g kg⁻¹ yr⁻¹, reaching an average of 339 g kg⁻¹ during the last five years (2017–2021) (Naeve and Miller-Garvin, 2022). Similarly, studies in USA and Argentina comparing old *versus* new soybean varieties showed that the yield increase of newer varieties was associated with a simultaneous decline in SPC (de Felipe et al., 2016; Rincker et al., 2014). If the declining trend in SPC persists as yield continues to increase, it may be difficult for soybean processors to produce a high-protein meal (Brumm and Hurburgh, 2006; Park and Hurburgh, 2002). Thus, it is relevant to examine opportunities that would generate higher seed yield without a concomitant SPC penalty.

A commonly acknowledged trade-off exists between SPC and seed yield, driven by both genetic improvements (de Felipe et al., 2016; Rincker et al., 2014) and upgraded management practices (Andrade et al., 2022; Assefa et al., 2019; Bellaloui et al., 2011; Bosaz et al., 2019; Mourtzinis et al., 2017). The genetic trade-off has been explained by interactions between high-protein and low-yield alleles at the quantitative trait loci (QTL) level (Chung et al., 2003). Genetic solutions to the SPC-yield trade-off have been explored, for example, by searching for QTLs whose two alleles alter protein but not oil (Lee et al., 2019; Phansak et al., 2016). Yield-improving management practices, such as early sowing date and crop rotation, also tend to decrease SPC, presumably because of a ‘dilution’ effect (Andrade et al., 2022; Bellaloui et al., 2011; Mourtzinis et al., 2017). An exception is N fertilizer application, which has been shown to increase both yield and SPC (Cafaro La Menza et al., 2017; Chiluwal et al., 2021; Figueiredo Moura da Silva et al., 2023). Yield is also greater with higher seasonal water availability, though the concurrent impact on soybean seed constituents is not clear, as previous studies have reported conflicting results (Grassini et al., 2021). One group of studies documented a simultaneous increase in yield and SPC due to irrigation (Foroud et al., 1993; Specht et al., 2001; Wijewardana et al., 2019). However, another group of studies reported a higher seed yield but lower SPC with irrigation (Dornbos and Mullen, 1992; Mertz-Henning et al., 2018; Rotundo and Westgate, 2010). Understanding the possible trade-off (or absence thereof) between yield and SPC when irrigation is relevant for high-yielding irrigated soybean systems in the USA, which currently account for ca. 12 % of U.S. soybean production (Hrozencik and Aillery, 2021), and for new areas where irrigated soybean production may expand in the future, such as the west-central U.S. Corn Belt, South America, and southern Europe.

The impact of water availability on soybean SPC has been investigated in a few controlled experiments where researchers applied different irrigation amounts among treatments (Mertz-Henning et al., 2018; Rotundo and Westgate, 2010; Wijewardana et al., 2019). An alternative approach would be to compare SPC between irrigated and rainfed soybeans based on seed samples collected from producer fields located in areas where both water regimes co-exist. If data on seed constituents and yield from many fields are available, and if those fields can be contextualized according to weather, soil, and management practices, such an approach would allow to assess the trade-off between seed yield and SPC due to irrigation. Although no experimental control is possible as in a typical replicated field experiment, a large number of fields, and their auxiliary management and biophysical data, can be useful to discern the main effect of irrigation influencing yield and seed constituents, providing a basis for more controlled and detailed studies aiming to identify the underlying physiological mechanisms. Though the

proposed producer-data driven approach has been used for understanding the causes of yield gaps (Andrade et al., 2022; Di Mauro et al., 2018; Rattalino Edreira et al., 2017), we are not aware of the application of this approach to investigate the on-farm *per se* influence of irrigation on both yield and seed constituents.

This foregoing approach would have the advantage of generating a regional-scale dataset for examining the degree to which the trade-off between yield and protein occurs when irrigation is applied, which thereby might lead to a better understanding of the conflicting results reported to date on this topic. Therefore, the objective of this study is to assess the trade-off between on-farm seed yield and SPC when irrigation is applied. With that objective in mind, we assessed the effect of irrigation on yield and seed constituents, focusing on SPC, as influenced by weather, soil, and management practices. We used a combination of two years of producer-reported data, *in-situ* seed collection from 268 soybean fields in Nebraska (USA), and crop modeling to estimate crop development stages. We hypothesized that SPC would likely be lower in irrigated *versus* rainfed fields because of higher seed yield that is commonly generated in irrigated fields and the trade-off typically observed between SPC and yield-improving management practices.

2. Materials and methods

2.1. On-farm database on yield, management practices, and seed constituents

Two years (2019 and 2020) of data were collected from fields in the state of Nebraska (USA), where ca. 2.2 M ha per year of soybean were harvested in the past three years (2020–2022) (USDA-NASS, 2023). Given that ca. 50 % of Nebraska’s annual soybean harvested area is irrigated (USDA-NASS, 2023), and that most farms have adjacent irrigated and rainfed fields (Grassini et al., 2014; Mourtzinis, Rattalino Edreira et al., 2018), Nebraska represents an ideal region for assessing the degree to which the trade-off between seed yield and SPC is influenced by irrigation. Our approach consisted of a combination of producer-reported data, *in-situ* seed collection, and crop modeling. Based on data from previous projects and information provided by extension educators and the Nebraska Soybean Board, we identified producers whose farms contained both irrigated and rainfed fields, totaling 84 irrigated-rainfed pairs, which result from the combination of producers and seasons (Fig. 1). On average, rainfed and irrigated fields on a given producer farm were located within a 10-km radius. Each producer was asked to provide data from three irrigated fields and from three (nearby) rainfed fields, but not consider fields that had been severely affected by unexpected adversities (*i.e.*, frost, hail, flooding, *etc.*) Likewise, rainfed corners of irrigated fields were not considered for our study. Although not all 84 producers supplied 6-field data in each year, about half (48 %) did supply data for one pair of irrigated-rainfed fields, another quarter (24 %) did so for two pairs, and a decile (10 %) did so for three pairs. The remaining producers (18 %) provided data from an unbalanced number of fields per water regime (*e.g.*, one irrigated and two rainfed fields). However, of the 2-year field total ($n = 268$), there was a near-equal split between irrigated (51 %) and rainfed (49 %) fields. Soybean was grown after prior maize crop, except for a small number of fields (4 %) that were grown after other crops such as wheat and dry beans.

For each field, we requested producers to report location, seed yield (at 130 g kg⁻¹ seed moisture content), and associated management practices, including total irrigation amount and method, sowing date, seeding rate, variety name and maturity group, row spacing, tillage method, nitrogen (N), phosphorous (P), potassium (K), sulfur (S), and zinc (Zn) fertilizer rates, plus any in-season foliar fungicide and insecticide applications (Supplementary Fig. S1, S2). To collect this information, producers completed a survey with the assistance of a local extension educator. We also requested producers to collect three seed samples from each of the reported fields during harvest time. To do so,

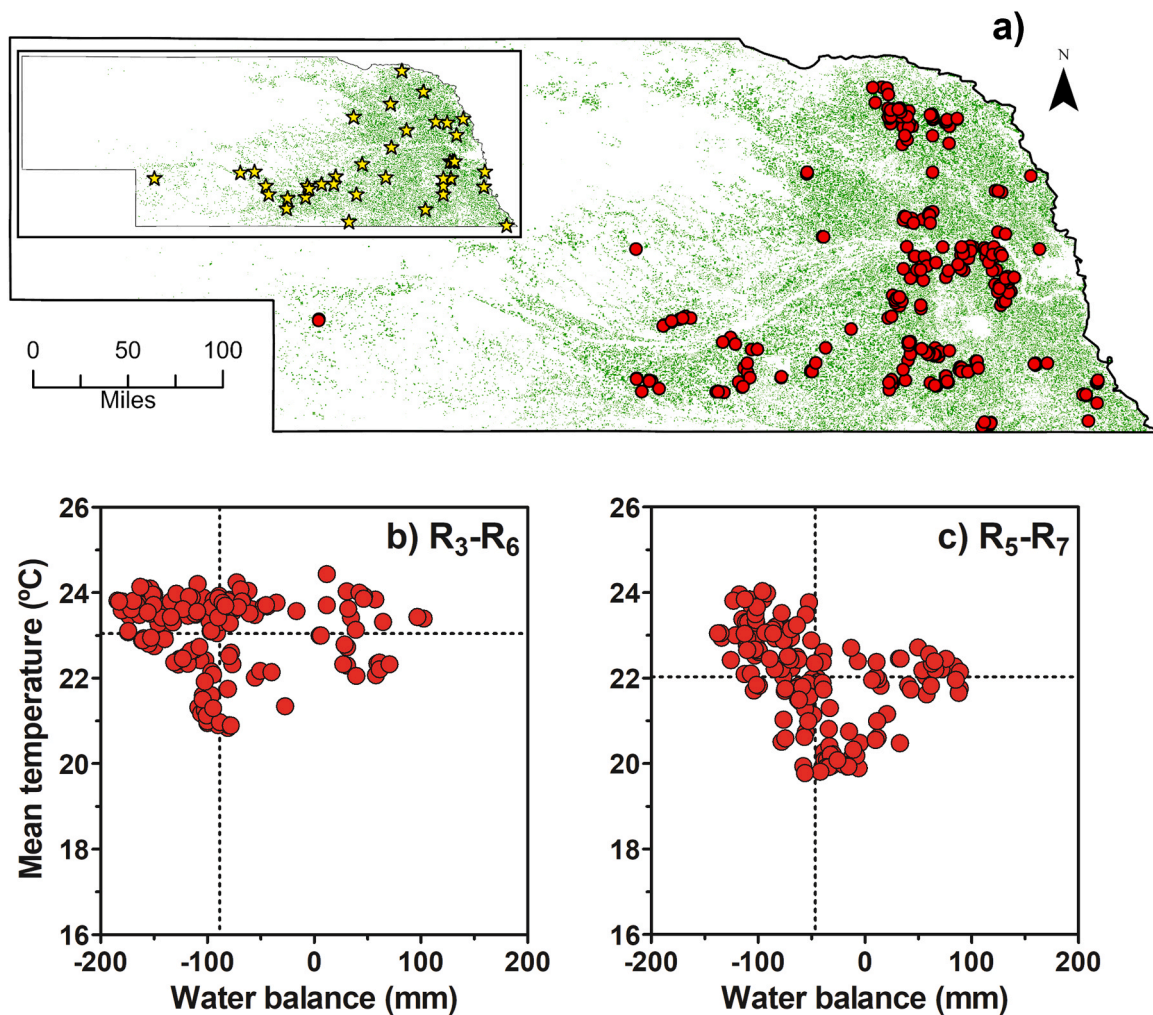


Fig. 1. (a) Location of the surveyed fields (solid circles) and weather stations (yellow stars) in Nebraska, USA, with the distributional density of soybean harvested area denoted by the green dots. Plots of location-specific average (solid circles) daily mean temperature *versus* water balance (precipitation – ET_0) during (b) the critical period (CP) for seed number determination and during (c) seed-filling (SF) phases of crop development. Horizontal and vertical dashed lines in the two plots denote the respective overall means for temperature and precipitation. Inset shows the location of the meteorological stations (yellow stars) used to retrieve daily weather data for each specific field *via* triangulation from the three nearby stations to each field.

we requested producers to follow a standardized protocol that included collection of three seed subsamples per field. These sub-samples were collected when roughly 25 %, 50 %, and 75 % of the field has been harvested. The collected seed samples were then placed in pre-labeled 1000-ml plastic jars and shipped to our laboratory. Samples were oven-dried and sent to the seed quality laboratory at the University of Minnesota for a multiple seed constituent analysis using near-infrared spectroscopy (PerkinElmer DA7250®) that generated values for SPC, SOC, and SCC. Variation in seed constituents among samples collected within the same field was very small as quantified using coefficient of variation (CV), averaging 1.3 %, 1.7 %, and 1.6 % for SPC, SOC, and SCC, respectively. Quantification of essential amino acids present in soybean seed is also relevant, as it defines the nutritional value of the meal (Bellaloui et al., 2011; Medic et al., 2014), so the samples were also analyzed for the concentration of 18 amino acids using near-infrared spectroscopy: methionine, cysteine, lysine, threonine, tryptophan, isoleucine, leucine, histidine, phenylalanine, valine, alanine, arginine, aspartic acid (*i.e.*, both aspartate and asparagine), glutamic acid (*i.e.*, both glutamate and glutamine), glycine, proline, serine, and tyrosine (Pfarr et al., 2018). Calibration equations were developed by the University of Minnesota in cooperation with PerkinElmer. Seed constituents were expressed at 130 g kg^{-1} seed moisture content. The economic value of soybean meal ($\$ \text{ Mg}^{-1}$) for swine nutrition was derived using

the model suggested by (Mourtzinis, Borg et al., 2018) based on SPC and amino acid concentration.

2.2. Retrieval of weather and soil data for each field

Soil organic matter and texture (clay and sand concentration) in the topsoil (0–30 cm depth) and plant available water holding capacity (PAWHC) were obtained for each field from the SSURGO database (Soil Survey Staff, 2023). Soil parameters varied within a narrow range, with clay and sand content averaging 290 and 120 g kg^{-1} , respectively, and with soil organic matter and PAWHC averaging 22.4 g kg^{-1} and 281 mm (Supplementary Fig. S1). Daily weather data, including incident solar radiation, maximum and minimum temperature, relative humidity, precipitation, and wind speed, were retrieved from 38 meteorological stations across Nebraska managed by the Automated Weather Data Network (<https://hprcc.unl.edu/awdn/>) (Fig. 1). Grass-referenced evapotranspiration (ET_0) was estimated using the FAO Penman-Monteith method (Allen et al., 1998). Weather data from up to the three stations nearest each given field were interpolated to create a synthetic daily weather dataset per field using inverse distance weighting (Yang and Torrión, 2013); (<https://hybridmaize.unl.edu/weatherDataUtilities>).

We used the SoySim model (Setiyono et al., 2010) to estimate the

calendar date of different crop growth stages, including beginning of pod setting (R_3), beginning of seed filling (R_5), full seed (R_6), and beginning of physiological maturity (R_7) (Fehr and Caviness, 1977). Simulations were based on the weather data specific for each field, and utilized producer-reported sowing date, seeding rate, and cultivar maturity group. Field-specific average mean daily temperature ($^{\circ}\text{C}$), average mean daily incident solar radiation ($\text{MJ m}^{-2} \text{d}^{-1}$), total precipitation (mm), and water balance (mm) were separately calculated for each of two crop reproductive phases: (i) the critical period (CP) for seed number determination from R_3 to R_6 (Monzon et al., 2021), and (ii) seed filling (SF) from R_5 to R_7 . The water balance was computed as the difference between total precipitation and ET_0 during each phase. These variables have been reported to influence seed yield and seed constituents in previous studies (Bellaloui et al., 2011; Bosaz et al., 2019; Di Mauro et al., 2018; Wijewardana et al., 2019; Zanon et al., 2016).

2.3. Data analysis

Averages of weather and soil variables, seed yield, and seed constituents (SPC, SOC, SCC, and amino acids) were calculated for each of the 84 rainfed-irrigated paired comparisons. As a first step, paired t-tests ($\alpha=0.05$) were used to understand the degree to which the comparison of irrigated and rainfed fields might have been influenced by potential intrinsic differences in biophysical (weather and soil) and management background (sowing date, nutrient fertilizer rates, etc.) between the paired water regimes. A Wilcoxon test was applied to those variables for which the data distribution deviated from normality, as evaluated using Shapiro-Wilk test. Categorical yes/no variables (e.g., fungicide application) were analyzed using Chi-square tests. A similar approach was used to assess differences in seed yield, seed constituents, and soybean meal value between paired water regimes. The magnitude of the irrigation-induced effect on seed yield and constituents may be influenced by management, soil, and weather conditions. For example, in water-limited environments, irrigation-mediated increases in seed yield could conceivably be amplified by higher fertilization rates, coarser soil textures, and greater incident solar radiation (Arora et al., 2011; Di Mauro et al., 2018; Zanon et al., 2016). Given that caveat, the difference between irrigated and rainfed fields relative to seed yield and seed constituents was calculated to identify relationships with the associated weather, and differences in management and soil factors. Statistical significance of those relationships was assessed using Pearson correlation analysis (*cor.test* procedure in R). As expected, weather variables did not differ significantly between paired water regimes ($P > 0.13$) located in proximity to each other on the same producer farm, so weather factors were averaged for those field pairs for use in the subsequent analysis.

Ultimately, the yield-SPC relationship was examined by calculating the difference in yield (ΔY) and SPC (ΔSPC) between the irrigated and rainfed fields that constituted an adjacent pair in each producer field. Those field pairs were subsequently grouped into two categories depending on whether the ΔY - ΔSPC value exhibited: (i) “no yield-SPC trade-off” (i.e., positive ΔSPC), or (ii) “trade-off” (i.e., negative ΔSPC). Thereafter, the two categories were compared to determine if variation in any management, soil, or weather factor was significantly associated with the yes - no trade-off categories. This assessment was conducted using an unpaired t-test analysis, though a Mann-Whitney test was alternatively used for non-normally distributed variables which were identified with a Shapiro-Wilk test. These tests were complemented with an analysis of whether SOC and SCC also differed between the two trade-off categories.

Seed yield and seed constituents are influenced by the genotype (Bellaloui et al., 2011; Bosaz et al., 2019). Unfortunately, it is difficult to control for this factor in analyses based on farmer data given the large number of varieties and their quick turnover. To assess any possible confounding effect of the genetic background on the irrigation effect that we assessed in the present study, we selected those rainfed-irrigated

paired comparisons that have the same variety. Following this approach, we selected 39 paired fields and assessed differences in seed yield and SPC between paired water regimes and analyze the yield-protein trade-off.

3. Results

3.1. Differences in seed yield and constituents between water regimes

The two crop seasons showed contrasting weather patterns: total seasonal precipitation (i.e., from sowing to physiological maturity) was 50 % greater in 2019 than in 2020 (326 mm versus 216 mm), whereas seasonal average temperature was just slightly lower in 2019 in comparison with 2020 (22.1 versus 22.6 $^{\circ}\text{C}$) (Fig. 1). Variation in weather, photoperiod, and variety maturity group led to large variation in crop cycle duration across fields, ranging from 84 to 128 days between emergence and R_7 . The average mean temperature during the reproductive phases ranged from 20.8 to 24.4 $^{\circ}\text{C}$ (CP) and 19.8–24.3 $^{\circ}\text{C}$ (SF), while the water balance ranged from -184–102 mm (CP) and -138–89 mm (SF). Furthermore, the average mean daily incident solar radiation ranged from 16.3 to 23.1 $\text{MJ m}^{-2} \text{d}^{-1}$ (CP) and 15.8–21.9 $\text{MJ m}^{-2} \text{d}^{-1}$ (SF) and precipitation from 10 to 297 mm (CP) and 6–295 mm (SF). Irrigation, applied by center pivot, ranged from 6 to 305 mm. Our surveyed fields adequately represented the range of management practices used by producers in their rainfed and irrigated fields (Supplementary Fig. S1, S2). No statistically significant differences in management practices and soil properties were detected between the paired irrigated-rainfed fields, except for slightly shorter cultivar maturity groups (-0.2 units) and higher soil organic matter (+1.8 g kg^{-1}) in the irrigated fields.

Average seed yield and SPC were both significantly higher in irrigated versus rainfed fields (Fig. 2). Although the average yield difference between irrigated and rainfed fields was substantial (+23 %), the change in SPC was much more modest (+1 %). Still, it was remarkable that despite the large yield enhancement arising from irrigation, SPC was not reduced (as initially hypothesized), but instead was significantly increased in most of the cases. Results derived from the analysis only considering pairs of rainfed-irrigated fields sown with same variety were almost identical to those derived from the whole database (Supplementary Fig. S3). The amino acid concentrations were also higher in irrigated versus rainfed fields, with positive changes ranging from +0.5 % (valine) to +2.3 % (cysteine), but with no changes occurring for three amino acids (tryptophane, isoleucine, and phenylalanine) (Fig. 3). Furthermore, irrigation increased the concentration in four of the five so-called limiting amino acids (methionine, cysteine, lysine, and threonine), which together with the overall increase in SPC, led to an enhancement of the resultant soybean meal value (from 310.4 to 312.4 \$ Mg^{-1}). Not unexpectedly, given the known negative correlation between seed protein and oil, SOC was significantly lower in irrigated versus rainfed fields ($P = 0.03$). No difference between water regimes was detected for SCC nor for seed mineral content ($P = 0.21$ and 0.16, respectively).

3.2. Factors influencing differences in seed yield and constituents between water regimes

There was a large variation in ΔY , ΔSPC , ΔSOC , and ΔSCC across field pairs (Fig. 2). For example, ΔY varies from zero to 2.5 Mg ha^{-1} , while ΔSPC ranged from -21.7–26.8 g kg^{-1} . We found that the water availability, solar radiation, temperature, and fertilizer application were associated with, and thus could explain or account for, the resultant variation in the seed yield and seed constituent differences between water regimes. For example, higher water deficits (i.e., low precipitation, and water balance, and high irrigation) led to a larger ΔY and a smaller ΔSOC , and resulted in no significant change in ΔSPC (Table 1). In contrast, greater solar radiation and mean temperature increased ΔY

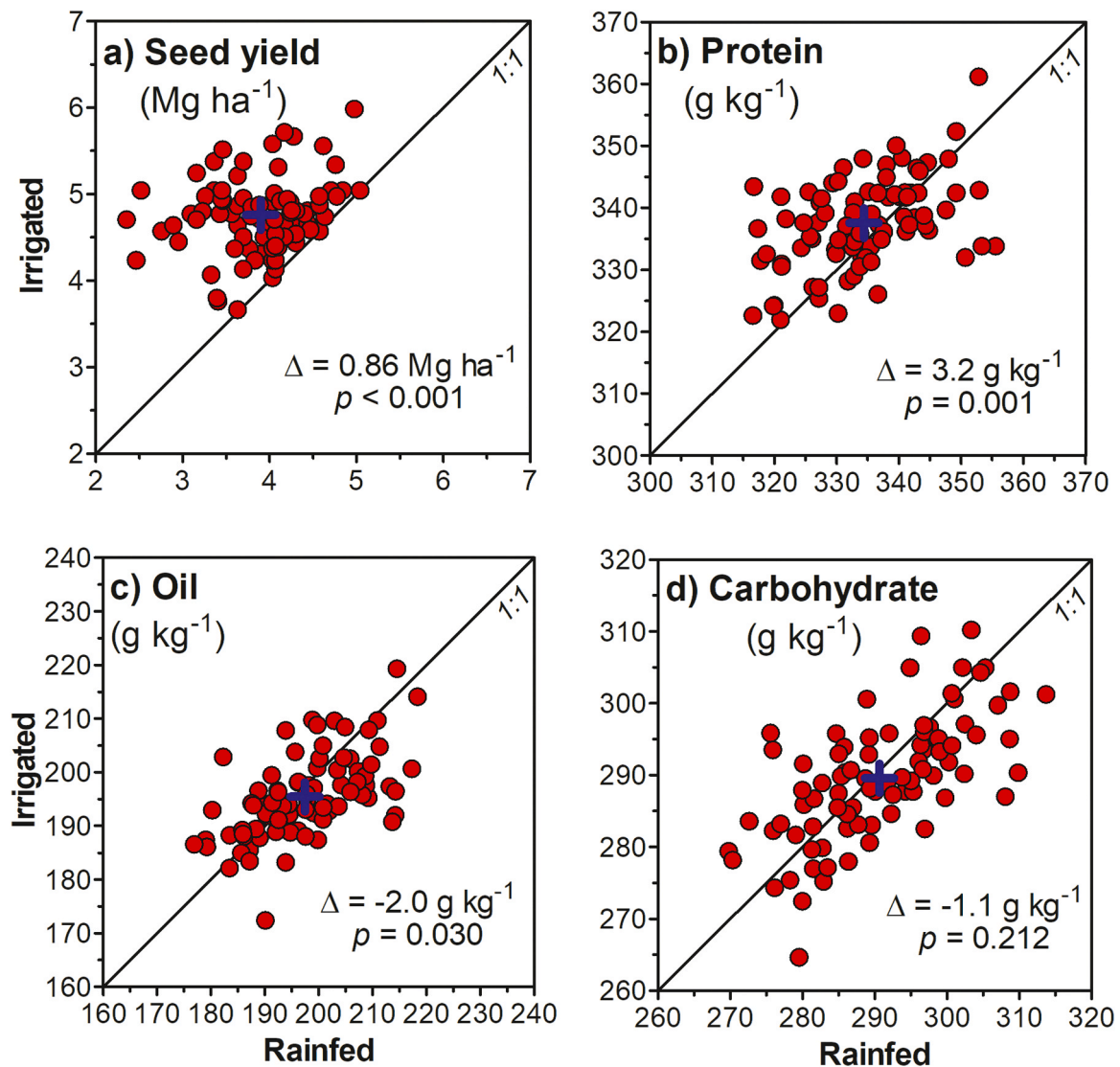


Fig. 2. Graphical depiction of seed (a) yield, (b) protein, (c) oil, and (d) carbohydrate values (solid circles) in the ($n = 84$) paired irrigated and rainfed soybean fields. The thick cross-hair symbol in each panel graphically denotes the experiment-wide average difference (Δ) between the two water regimes that is shown at the bottom right of each panel, along with the associated p value for a t-test evaluation of the significance of the degree of departure of the data points from the diagonal 1:1 line, which is a graphical representation of the null hypothesis of no difference between the two water regimes.

but resulted in a reduced ΔSPC . Interestingly, higher K and S fertilizer in irrigated *versus* rainfed fields led to larger ΔY , whereas higher P fertilizer application decreased ΔSPC . With respect to ΔSCC , its correlations were similar to the ΔY correlations, but were weaker. Other weather, soil, and management factors, including the maturity group, were not significantly associated with, and thus were not meaningful relative to accounting for the differences in yield and seed constituents between water regimes (Supplementary Table S1).

3.3. Assessing the magnitude of any trade-offs between seed yield and seed constituents

The impact of irrigation on the trade-off between seed yield and SPC was assessed by analyzing the relationship between ΔY and ΔSPC (Fig. 4). Two-thirds of the irrigated-rainfed pairs exhibited an increase in both seed yield and SPC (*i.e.*, no trade-off), while a trade-off was apparent between ΔY and ΔSPC in the remaining fields. Similar patterns were observed when the analysis was based on pairs of irrigated-rainfed fields that were shown with the same variety (Supplementary Fig. S3).

We also examined the factors that might account for the contrasting

trade-off responses (Table 2). We found no differences in management and soil variables, and little differences in weather factors, between the two trade-off categories. The trade-off category fields (for which an irrigation-driven seed yield enhancement but also SPC reduction was observed) were associated with environments with greater solar radiation and higher temperature during SF – conditions that were conducive for higher SOC and SCC.

4. Discussion

An analysis of producer-reported data, *in-situ* seed samples, and crop modeling was used for the first time to assess the degree to which yield-SPC trade-off is influenced when yield increases are generated by irrigation. Assessing the impact of irrigation on yield and many seed constituents across 268 surveyed fields with varying environmental and management backgrounds provided an extensive on-farm dataset that offers analytic advantages compared to previous studies conducted using a more modest number experimental station field sites in specific site-years (Foroud et al., 1993; Mertz-Henning et al., 2018; Rotundo and Westgate, 2010; Specht et al., 2001). Overall, in the majority (2/3) of

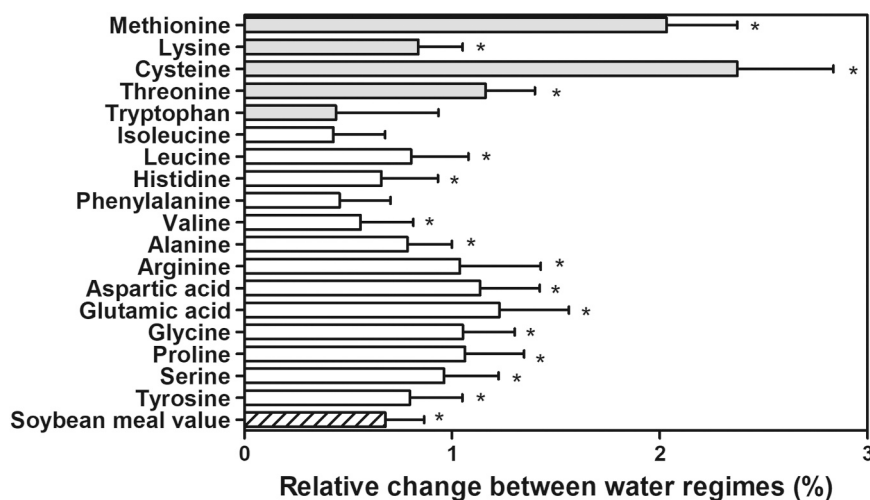


Fig. 3. Relative change between irrigated and rainfed soybean fields relative to amino acid concentrations (open bars) and soybean meal value (hatched bar). Grey bars depict the five limiting essential amino acids. Horizontal whiskers in each bar denote the standard error of the mean. Bars capped by an asterisk indicate that the relative change between the two water regimes was statistically significant ($p < 0.05$).

Table 1

Pearson's correlation coefficients for irrigated-rainfed differences (Δ) in seed yield and seed constituents *versus* management, soil, and weather factors. Weather factors were analyzed for two crop reproductive phases: the critical period (CP) for seed number determination and seed filling (SF). Only management, soil, and weather factors that had statistically significant correlations with at least one dependent variable are shown here. An extended version of the table is provided in [Supplementary Table S1](#).

| | ΔY | ΔSPC | ΔSOC | ΔSCC |
|---------------------------|------------|--------------|--------------|--------------|
| <i>Management factors</i> | | | | |
| Irrigation | 0.55 ** | | -0.38 ** | 0.28 ** |
| Δ MG | | | | 0.22 * |
| Δ P | | -0.24 * | | 0.27 ** |
| Δ K | 0.28 ** | | | |
| Δ S | 0.27 * | | | |
| <i>Weather factors</i> | | | | |
| R_{CP} | 0.61 ** | -0.23 * | | 0.32 ** |
| R_{SF} | 0.63 ** | | | 0.31 ** |
| T_{CP} | 0.30 ** | | | |
| T_{SF} | 0.44 ** | -0.37 ** | | |
| P_{PCP} | -0.23 * | | 0.31 ** | |
| P_{PSF} | -0.43 ** | | 0.23 * | -0.23 * |
| WB_{CP} | -0.42 ** | | 0.29 ** | -0.29 ** |
| WB_{SF} | -0.55 ** | | 0.22 * | -0.30 ** |

Dependent variables: irrigated-rainfed yield difference (ΔY), protein concentration (ΔSPC), oil concentration (ΔSOC), and carbohydrate concentration (ΔSCC). Independent variables: irrigation, mean daily incident solar radiation (R), mean daily temperature (T), total precipitation (Pp), total water balance (WB), and irrigated-rainfed differences in maturity group (ΔMG), phosphorus fertilizer (ΔP), potassium fertilizer (ΔK), and sulfur fertilizer (ΔS). Asterisks indicate significance at $p < 0.05$ * and $p < 0.01$ **.

paired irrigation *versus* rainfed field cases, irrigation increased both seed yield and SPC while concurrently reducing SOC (Figs. 2 and 4). Except for tryptophan, the concentration of the other four limiting essential amino acids (methionine, cysteine, lysine, and threonine) increased in irrigated fields (Fig. 3), leading to improvements in the quality of the protein (Bellaloui et al., 2011; Medic et al., 2014). Irrigation thus increased the soybean meal value that is routinely calculated for use in swine nutrition, which would allow irrigated soybean producers to access better prices offered by soybean seed processors (Mourtzinis, Borg et al., 2018).

Although some management factors may exhibit confounding effects with respect to their influence in irrigated *versus* rainfed fields, we have evidence to dismiss these possible factors. For example, NO_3-N is

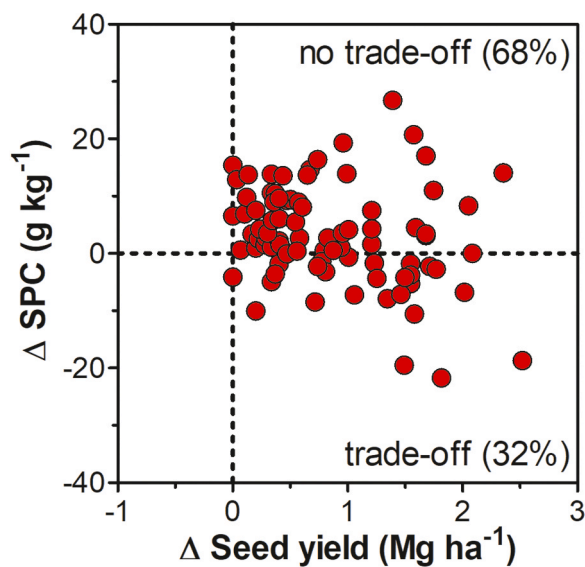


Fig. 4. Irrigated-rainfed differences in seed protein concentration (ΔSPC) and seed yield (ΔY). Each datapoint corresponds to an irrigated-rainfed paired comparison ($n = 84$). The percentage of data points falling in the upper and lower fraction of the graph are indicative of the proportion of paired fields exhibiting either no-trade off or a trade-off between ΔSPC and ΔY .

frequently present in Nebraska ground water, and thus an irrigated (but not rainfed) crop would be supplied with N applied *via* irrigation water. However, that amount was expected to be relatively small in our study areas (Grassini et al., 2014). Likewise, irrigated fields could present better soils, as was documented in our study by higher soil organic matter concentrations in irrigated than in rainfed fields (Supplementary Fig. S1), which is consistent with previous studies (Grassini et al., 2015). However, the impact of these factors is expected to be relatively small and not sufficient to explain the lack of a trade-off between yield and SPC. Indeed, none of them differed between trade-off and no trade-off categories (Table 2). Also, N fertilizer and N balance in the prior maize crop are larger in irrigated fields (Tenorio et al., 2020). Still, empirical evidence shows that N management in maize does not affect the seed yield of the following soybean crop (Correndo et al., 2022). Furthermore, SPC is also affected by the genotype (Bellaloui et al., 2011; Bosaz et al., 2019), thus confounding effects with irrigation. However,

Table 2

Comparison of the non-trade-off versus the trade-off categories of paired fields (as shown in Fig. 4) relative to the solar radiation and temperature values that prevailed during the critical period (CP) and seed-filling (SF) phases of soybean reproductive development. These were the only management, soil, and weather factors that significantly differed between trade-off categories ($p < 0.05$).

| Variable | No trade-off (n = 57) | Trade-off (n = 27) | p-value |
|---|--------------------------|-----------------------|---------|
| <i>Weather factors</i> | | | |
| R _{CP} (MJ m ⁻² d ⁻¹) | 19.6 | 20.5 | 0.015 |
| R _{SF} (MJ m ⁻² d ⁻¹) | 18.3 | 19.6 | 0.007 |
| T _{SF} (°C) | 21.7 | 22.5 | 0.007 |
| <i>Seed constituents</i> | | | |
| Δ SOC (g kg ⁻¹) | -6.4 | 3.0 | <0.001 |
| Δ SCC (g kg ⁻¹) | -3.2 | 3.3 | <0.001 |

R: mean daily incident solar radiation; T: average mean daily temperature; ΔSOC: irrigated-rainfed difference in seed oil concentration; ΔSCC: irrigated-rainfed difference in carbohydrate concentration.

our analysis of a subset of rainfed-irrigated fields that were sown with the same varieties showed near identical results to those derived using the whole database (Supplementary Fig. S3). Thus, we conclude that irrigation can help maintain or even increase SPC compared to rainfed soybeans. Together with N fertilizer addition (Cafaro La Menza et al., 2017; Chiluwal et al., 2021; Figueiredo Moura da Silva et al., 2023), we are not aware of any other management practices that can lead to simultaneous increases in seed yield and SPC.

One-third of our irrigated-rainfed field comparisons exhibited a yield-SPC trade-off (Fig. 4). These cases were associated with favorable environmental conditions for seed oil synthesis and deposition, which in this study were identified as higher incident solar radiation and warmer temperature during the SF phase (Table 2). This finding was consistent with previous positive relationships between SOC and temperature and solar radiation reported in the literature (Bianculli et al., 2016; Carrera et al., 2009; Naeve and Huerd, 2008; Piper and Boote, 1999). Oil synthesis and accumulation in seed depend on the photosynthates generated during the SF, whereas SPC also relies on carbon and N remobilization (Bosaz et al., 2019; Rotundo et al., 2011). Therefore, under conditions that promote photosynthesis (*i.e.*, higher temperature, solar radiation, and water availability), oil deposition is favored, and protein concentration decreased due to a dilution effect (Rotundo and Westgate, 2009).

Irrigation did not lead to a trade-off between yield and SPC in two-thirds of the fields, which could be also explained (Fig. 4). First, irrigation can reduce canopy temperature because greater soil water evaporation and canopy transpiration generate a “cooling effect”. Therefore, the reduction in canopy temperature would decrease seed oil synthesis, which, because of a negative correlation with seed protein deposition, would increase SPC (Pandey et al., 1984; Rotundo et al., 2011). Second, irrigation can increase the overall N supply by increasing soil N mineralization, especially with higher soil organic matter concentrations, such as those we observed in irrigated compared to rainfed fields (Reussi Calvo et al., 2018). Furthermore, irrigation can also increase N supply by improving the biological N fixation, which is usually reduced under water-limited conditions (Purcell et al., 2004; Serraj et al., 1999). For example, irrigated soybean exhibited higher nodule number, dry weight, and biological N fixation compared to water-limited plants (Serraj et al., 1999; Lumactud et al., 2023). Therefore, irrigation could enhance both N sources (*i.e.*, N from soil organic matter mineralization and biological N fixation), increasing the overall plant N uptake, which is the ultimate mechanism that could lead to high seed yield and SPC (Bosaz et al., 2019; Fabre and Planchon, 2000; Sinclair et al., 2007).

One can hypothesize that the trade-off between seed yield and SPC might be mitigatable when the management factors associated with the yield improvement simultaneously increase N supply. This conjecture is

consistent with the concomitant increase in seed yield and SPC in response to N fertilizer addition that has been reported by previous studies in soybean (Cafaro La Menza et al., 2017; Chiluwal et al., 2021; Figueiredo Moura da Silva et al., 2023). Also consistent with this hypothesis is that other management practices are not expected to influence N supply, such as sowing date, maturity group, row spacing, and fungicide application, all of which typically result in higher yield and lower SPC (Andrade et al., 2022; Assefa et al., 2019; Bellaloui et al., 2011; Bosaz et al., 2019; Mourtzinis et al., 2017). Similar findings in relation to the influence of management factors on yield and SPC have been reported for maize, with lower grain N concentration when yield was increased *via* improved hybrids and/or higher plant density, but higher grain N concentration and grain yield with increasing N fertilizer rate (Tenorio et al., 2019).

In our study, we observed positive and negative changes in ΔSPC across a wide range of conditions representative of the US soybean production region (Rattalino Edreira et al., 2017, 2020). Our results align with results from field experiments in Nebraska using sprinkler irrigation (Specht et al., 2001) and more controlled experiments conducted in small plots or pots with drip irrigation (Foroud et al., 1993; Wijewardana et al., 2019). However, our findings differ from other studies that reported increased yield and decreased SPC in response to irrigation (Dornbos and Mullen, 1992; Mertz-Henning et al., 2018; Rotundo and Westgate, 2010). One can speculate on the causes for these contrasting results. Mertz-Henning et al., (2018) reported the overall yield-SPC relationship across years. However, analysis of the individual seasons revealed higher SPC in response to irrigation in the cooler season, but lower SPC in the other two (warmer) crop seasons, which aligns with our findings (Table 2). Similarly, Dornbos and Mullen (1992) and Rotundo and Westgate, (2010) observed interactions between irrigation and temperature on SPC, with lower SPC observed with irrigation, but this effect depended on temperature, with lower SPC at higher temperatures and *vice versa*. Indeed, Rotundo and Westgate (2010) reported that irrigation increased SPC for one cultivar (PR142) in the year with cooler temperatures (2007). Likewise, Carrera et al. (2009) reported that a combination of large water balance (> 70 mm) and high temperature during the reproductive period (R₁-R₇) led to higher SOC and lower SPC, which is attributable to higher oil synthesis and concomitant reduction in SPC due to a dilution effect (Rotundo and Westgate, 2009, 2010). Given this experimental evidence, we then speculate that interactions between temperature and irrigation on SPC may explain the contrasting results reported in previous studies.

5. Conclusions

We used a novel approach to understand possible trade-offs between seed yield and protein concentration with irrigation. This approach included producer-reported data, *in-situ* seed samples, and modeling. We found that irrigating in Midwestern USA water-limited environments increased both seed yield and protein concentration in most fields in a 2-year timeframe. Furthermore, irrigation also increased the concentration of four out of the five essential amino acids and the soybean meal value. Trade-offs between these two variables were only apparent in minority field cases where the production environment favored seed oil synthesis (*i.e.*, warmer temperatures and higher solar radiation). Irrigation is one of the practices that, together with the addition of nitrogen fertilizer, can lead to simultaneous increases in yield and seed protein concentration in soybean.

CRedit authorship contribution statement

Walter D. Carciochi: Conceptualization, Formal analysis, Writing – Original Draft; **Patricio Grassini:** Conceptualization, Writing – Original Draft, Formal analysis, Investigation, Funding acquisition; **Seth Naeve:** Resources, Writing – Review & Editing; **James E. Specht:** Investigation, Writing – Review & Editing; **Mitiku Mamo:** Investigation, Writing –

Review & Editing; **Ron Seymour**: Investigation, Writing – Review & Editing; **Aaron Nygren**: Investigation, Writing – Review & Editing; **Nathan Mueller**: Investigation, Writing – Review & Editing; **Sarah Sivits**: Investigation, Writing – Review & Editing; **Christopher Proctor**: Investigation, Writing – Review & Editing; **Jenny Rees**: Investigation, Writing – Review & Editing; **Todd Whitney**: Investigation, Writing – Review & Editing; **Nicolas Cafaro La Menza**: Conceptualization, Formal analysis, Investigation, Writing – Original Draft, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare no competing interest.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fcr.2023.109163](https://doi.org/10.1016/j.fcr.2023.109163).

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