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Empirical modeling of the impact of Mollisol soils variation on performance of Cuphea: a potential oilseed crop

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Abstract

Production potential of many soils is affected by low supply of nutrients due to adverse constraints or spatio-temporal variation of soil physico-chemical properties. New oilseed crops differ in their nutrient needs for maximum performance in different soils and may not be able to economically compete with grain crops for fertile land. Spatial variation in physico-chemical properties within and among four Mollisols during two contrasting cropping seasons accounted for significant and decreasing amounts of variation in crop performance quantified by seed yield, oil content and oil yield in Cuphea (*Cuphea viscosissima* Jacq. x *Cuphea lanceolata* W.T. Aiton; PSR23), a semi domesticated oilseed crop. Spatially demarcated 36 grids within soil series accounted for more variation in crop performance and reacted more significantly to temporal variation than soil series. Nutrient ratios of carbon, nitrogen, phosphorus, and sulfur in seed were slightly better predictors of oil content and oil yield than those in soil. Soil chemical properties, including nutrient contents, soil pH, water, and electrical conductivity, when used as covariates or predictors in calibration and validation partial least squares regression models, provided new insights into the variation structure and prediction of crop performance. Predictive models may help design management strategies to optimize oil content and oil yield of oilseed crops on different soil types.

Keywords: Mollisols, nutrients, oilseed, soil series, spatial variation, validation models.

Introduction

Production potential of many soils around the world will continue to be impacted by the low supply of nutrients due to adverse soil physical and chemical constraints (Dobermann and Cassman, 2002), while it is highly likely that increases in future food production will largely come from today's most intensively cultivated agricultural lands. Nevertheless, farmers will continue to search for reliable management practices in order to better account for spatial and temporal variation in indigenous nutrient supply and crop nutrient demand (Jaradat and Weyers, 2011). Maximum production potential of many field crops may not have been achieved in the past due to insufficient characterization of spatial variation in indigenous nutrient supply (including sampling and laboratory errors), and yield goals (Jackson 2000). In addition, there is inadequate understanding of soil spatial cause–effect relationships that can be quantified, generalized and extrapolated within and among different soil series (Castrignanò et al., 2000). The lack of multivariate response functions that can estimate yield response to native soil fertility and other soil characteristics for a new crop species may hinder the development and use of variable rate fertilizer application guidelines (Bayer et al., 2012). Therefore, modeling the relationship between soil physico-chemical properties and crop yield cannot be overemphasized (Shattar and McBratney, 1999). This approach is necessary to identify factors, whether manageable or not, causing yield variation; some of these factors may be highly variable but may not affect yield potential of some crops. Historically, however, research on plant nutrition was aimed primarily at preventing loss of on-site productivity, and developed appropriate soil and crop management practices to provide for ample nutrient supply to the current crop without excessively mining soil nutrient resources (van Noordwijk and Cadesch, 2002). The importance of oilseed crops as a source of bioenergy and other industrial products is rising and the consumption of their oil has increased by about 50% during the past decade (Haslam and Michaelson, 2013). However, the growth in land area planted to oilseed crops is expected to slow down markedly due to high marginal costs of land expansion, environmental constraints and, partly to current sustained profitability of competing food crops (Nad et al., 2001). New oilseed crops, such as *Cuphea* spp., may differ in their nutrient needs for maximum performance in different soils and may not be able to economically compete with grain crops for fertile land, especially in developed countries where marginal land cost is high (van Noordwijk and Cadesch, 2002). Therefore, it is prudent to explore how this and similar new oilseed crops can be expanded into more marginal land and how their productivity can be maintained under diverse environments. Although the environment has a significant influence on the final oil content of the seed (Ngezimana, 2012), spatial differences in the soil physico-chemical properties may cause yield variation even in a seemingly homogenous land area (Hakojärvi et al., 2013). The semi-domesticated Cuphea selection (i.e., PSR23) is a potential new oilseed crop whose oil is being used in the food and cosmetic industries (Berti and Johnson, 2008), and potentially as a jet fuel and in industrial lubricants. This selection, when compared to other Cuphea spp. tended to exhibit a wide range of adaptability to climate (total growing degree days ranged from 1057 to 1561, and total rainfall during the growing season of May-September from 221to 587 mm) and soil conditions (Osco silt loam, Clarion loam, Barnes loam, and Perella silt-clay loam soils) across the upper Midwest of the US (Kim et al., 2011). Research results on optimum soil fertility for Cuphea's growth and development and for seed and oil yield were not conclusive (Berti and Johnson, 2008), while its low harvestable seed yield could be partly attributed to its low water use efficiency (1.5-2.0 kg ha^{-1} seed mm^{-1} of water) which was estimated at about 50% of other oilseed crops (e.g., 2.8 kg ha^{-1} seed mm^{-1} of water) such as soybean and sunflower (Sharratt and Gesch, 2004). Consequently, its nutrient use efficiency is assumed to be lower than those oilseed crops, and if improved, could reduce fertilizer inputs, decrease nutrient loss, and enhance its seed and oil yields (Baligar et al. 2001). A Cuphea ideotype is envisaged as one that can fit into, and add diversity to the current 2-year crop rotation, and as having a moderate-to-low nutrient requirements, a low seeding rate, rapid growth cycle, reaching maturity in about 100 days, a high resistance of capsules to dehiscence, and an oil content of about 35-40% (Jaradat, 2012). The objectives of this study were to (1) quantify the effects of spatial variation in physico-chemical properties within and among four soil series during two contrasting cropping seasons on Cuphea's performance as measured by seed weight, seed yield, oil content and oil yield, (2) discriminate between soil series on the basis of their physico-chemical properties and identify latent variables which account for maximum variation, (3) explore the functional relationships between nutrients and between nutrient ratios in soil and seed, and implications for optimized oil content, and (4) calibrate and validate partial least squares regression models to predict Cuphea's performance under spatio-temporal variation.

Results

Multivariate assessment of soil spatial variation

Bivariate relationships between horizontal and vertical electrical conductivities (EM_H and EM_V, respectively) and their joint relationship with pH (Fig. 1A) averaged over soils and years and for each soil series revealed major differences between and within soils; with 73% of the r-values being significant ($p<0.05$). All data points depicting the relationship between EM_H and EM_V were above the diagonal and both were positively correlated (r = 0.39 – 0.94; $p<0.05$; Fig. 1A) with no clear association with pH estimates. Barnes and Barnes-Buse had below average, while Hamerly and Parnell had above average means of EM_H and EM_V. The distribution of grids within the polygon indicated the presence of a group of Barnes and Barnes-Buse at the lower end, a group of Hamerly and Parnell at the upper end, and an intermediate group of mostly Hamerly grids in between. Most pH estimates ranged from 7.7 to 7.9; however, there were some soil pockets with lower (~6.5) and larger (>0.8.0) estimates. The lack of significant relationships between EM_H and EM_V with pH (in addition to EM_H with ECe) differentiated Barnes and Barnes-Buse from Hamerly and Parnell; while, r-values between ECe and each of EM_V and pH were variable among soils. Similarly, bivariate relationships between EM_H and EM_V and their joint relationship with ECe (Fig. 1B) averaged over soils and years and for each soil series revealed major differences between and within soils; with 70% of the r-values being significant ($p<0.05$) when their relationships with soil nitrogen (N), organic carbon (OC), and inorganic carbon (IC) are considered. The ECe displayed a wide range of associations with EM_H and EM_V across soils as depicted in Fig. 1B, as well as with N (r = -0.65 to 0.70), OC (r = -0.65 to 0.69) and IC (r = -0.47 to 0.72) in different soils. When averaged over all soils, the r-values between all four soil attributes (i.e., EM_H, EM_V, ECe, and pH) with N (r = 0.46 to 0.78) and OC (r = 0.50 to 0.81) were all positive and significant ($p<0.05$) except with pH (r = -0.20 to 0.17; $p>0.05$); whereas, their r-values with IC were not significant (r = -0.20 to -0.28; $p>0.05$) except with pH (r = 0.71; $p<0.05$). Barnes and Barnes-Buse displayed similar relationships between AMH and N, but differed in several others (e.g., ECe and pH with N; EM_H, EM_V and ECe with IC; and EM_H, ECe and pH with OC); whereas Hamerly and Parnell displayed more similarities and a few dissimilarities (ECe and pH with N and OC) between these soil attributes. Statistical assessment of soil spatial variation (Table 1) indicated that variation within and among soils in texture (i.e., clay, silt and sand) was negligible; however, there were slight differences between soils in the level of variation in these soil components. The C.V.% for clay in Barnes, Barnes-Buse, Hamerly, and Parnell were 15.4, 13.5, 10.6, and 11.0%, respectively; the respective values for silt were 21.4, 8.8, 8.8, and 6.1%; and for sand, 7.4, 8.8, 10.8, and 4.3%. However, variation within and among soil series for most other variables was the norm as expressed by significant ($p<0.05$) or marginally ($p<0.09$) significant F-values for most (64%) variables. The variation among soils for components of soil electrical conductivity (i.e, pH, ECe, ECa, including EM_H and EM_V), five nutrients (Cu, Fe, S, and Zn), and one nutrient ratio (P:S), was smaller than their respective level of variation within soils. Carbon and N-related variables exhibited the largest levels of variation among soils; whereas, K was the most variable among soils and among nutrients. Statistically, spatial variation within soils was larger in Barnes (68% of variables) and Parnell (60%), than in Hamerly (52%) and Barnes-Buse (48%). All four soils displayed large within soil variation in soil water content, and C- and N-related variables, as compared to the small variation in components of soil electrical conductivity. Soils differed markedly as to nutrients exhibiting significance levels of variation. A block of four nutrients (Ca-Mg-S-Zn) in Barnes, two (Fe-Zn) in Barnes-Buse, one (Mg) in Hamerly, and three (Cu-P-S) in Parnell, in addition to K in all soils, indicated the level of statistical variation within these soils. Nutrient ratios, involving C, N, P and S, showed within-soil significant differences (60%) for all soils (C:N and C:P), for Barnes (N:S and P:S), Hamerly (N:P), and Parnell (P:S).

Spatial variation in crop performance

Basic statistics for oil content (Fig. 2A) and oil yield (Fig. 2B) estimated on seed harvested from each grid and soil series in 2005 and 2006 illustrate the large spatial (and temporal) variation for these variables. The 1-D plot for each variable displayed sharp fluctuations within short distances among and within years. The variability in oil content (mean CV% was 2.9 in both years) was more conservative than variability in oil yield (see below). Differences in oil content between soil series within years were minimal; however, significantly ($p<0.05$) larger oil content was achieved by the crop in 2006 than in 2005 which was largely due to greater seed yield. Seed produced on all soils had statistically similar oil content in each year; whereas average oil content in 2006

Table 1. Analyses of variance (*F*-value and *p*-value) for soil variables and nutrient ratios among and within four Mollisol soils at the Swan Lake Research Farm, Morris, MN, USA.

Variable	All soils		Barnes		Barnes-Buse		Hamerly		Parnell	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Clay	1.99	0.16	3.12	0.11	0.05	0.86	2.05	0.16	0.28	0.61
Silt	1.49	0.22	0.98	0.34	1.62	0.23	1.87	0.18	0.09	0.92
Sand	0.17	0.68	0.04	0.84	0.49	0.49	0.06	0.82	0.62	0.45
Soil water	49.3	0.001	12.9	0.003	58.4	0.001	157.1	0.001	260.4	0.001
NH_4^+	84.7	0.001	25.5	0.001	22.6	0.001	46.2	0.001	7.6	0.02
NO_3^-	145.5	0.001	134.3	0.001	3.6	0.08	101.2	0.001	167.1	0.001
ECe	1.3	0.2	2.5	0.14	0.4	0.5	0.99	0.3	13.6	0.004
ECa	1.78	0.11	1.5	0.25	5.2	0.03	1.25	0.15	2.7	0.07
EM_V	0.55	0.4	1.7	0.22	1.9	0.2	0.02	0.9	3.9	0.07
EM_H	1.2	0.3	1.3	0.27	6.2	0.03	1.83	0.2	0.2	0.7
pH	16.6	0.001	62.6	0.001	3.1	0.1	14.6	0.001	0.3	0.6
N%	17.6	0.001	11.2	0.005	10.3	0.007	51.5	0.001	54.9	0.001
C%	153.5	0.001	577.2	0.001	561.6	0.001	212.9	0.001	1031	0.001
IC%	8.9	0.003	13.8	0.003	0.96	0.3	5.3	0.03	0.3	0.6
OC%	11.5	0.001	9.6	0.009	12.9	0.004	23.1	0.001	50.5	0.001
Ca	3.1	0.08	8.5	0.01	1.05	0.3	1.8	0.2	1.2	0.3
Cu	0.07	0.7	0.32	0.58	0.94	0.3	0.01	0.9	3.5	0.09
Fe	0.04	0.8	0.78	0.39	8.1	0.02	0.62	0.4	0.08	0.8
K	9.6	0.002	4.9	0.05	4.7	0.05	15.9	0.001	11.3	0.007
Mg	6.2	0.01	9.9	0.008	2.9	0.1	4.1	0.05	1.2	0.3
Mn	1.1	0.3	2.8	0.11	0.05	0.9	0.7	0.4	0.17	0.7
P	4.1	0.05	1.7	0.22	0.46	0.5	1.7	0.2	5.3	0.05
S	0.51	0.5	5.8	0.03	0.51	0.5	0.3	0.6	13.4	0.004
Zn	0.92	0.3	3.7	0.07	25.9	0.001	0.2	0.7	0.01	0.9
C:N	47.5	0.001	10.2	0.007	10.7	0.006	30.5	0.001	23.8	0.001
C:P	74.7	0.001	184.4	0.001	196.5	0.001	109.7	0.001	51.4	0.001
N:P	3.5	0.06	0.48	0.5	0.03	0.9	3.1	0.09	0.5	0.5
N:S	2.9	0.09	3.4	0.08	0.08	0.8	2.6	0.1	0.2	0.7
P:S	0.5	0.72	15.9	0.001	0.54	0.85	0.7	0.92	28.2	0.001

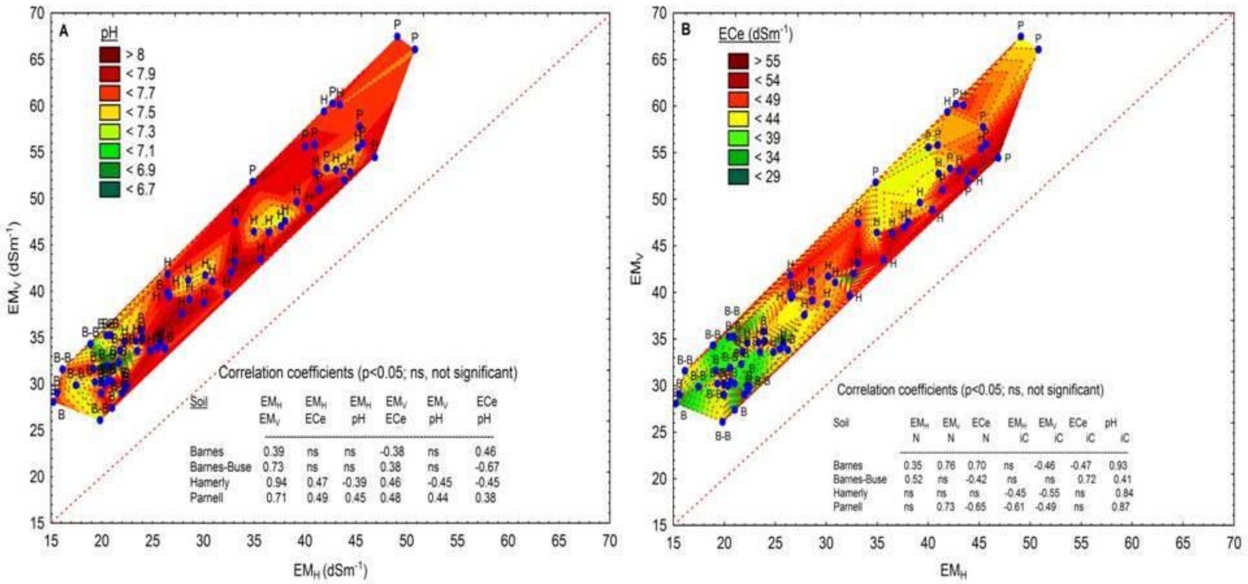

Fig 1. Relationships between each of EM_H and EM_V and pH (A), ECe (B) and three soil attributes (N, IC and OC) in All four Mollisols, and each of Barnes (B), Barnes-Buse (BB), Hamerly (H), and Parnell (P) averaged over two growing seasons. (ns: not significant at p=0.05).

was significantly ($p<0.05$) larger than in 2005 (Fig. 2A). The variability in oil yield was large in both years (mean CV% was21.6 in 2005 and 29.5 in 2006); oil yield was significantly and negatively correlated (r -0.76; $p<0.001$) with oil content when averaged over years; however, it was positive but not significant in each year. There were significant differences between soil series in oil yield between and within years (Fig. 2B). Also, there were large CV% values for Hamerly in 2006 (31.6), and Parnell in both years (30.8 and 27.1%); while, the smallest value was 6.7% for Hamerly in 2005. The bivariate negative relationship between oil content and oil yield, and their positive joint relationship with seed yield of Cuphea (Fig. 3) suggest that oil yield in excess of 220 L ha^{-1} can be produced provided that a minimum of 28% oil content is maintained in seed, and if soil and annual variation are at minimum. Three groups of grids within soil series can be identifies as to the relationship between seed yield and oil content; the first group produced low seed yield and high oil content; the second produced high seed yield and low oil content; while the intermediate was in between and exhibited larger variation than the other two extremes. The polygon suggested that most high oil yield came from Hamerly, followed by Barnes. In addition, the data suggested that different levels of oil yield can be produced at the same level of seed yield, or the same level of seed yield can produce increasing amounts of oil as a result of higher oil content. The boundary of the polygon is demarcated by soil grids that produced extreme and variable combinations of seed yield, oil content, and oil yield.

Statistical and functional attributes of nutrients

Several statistical procedures helped to describe univariate, bivariate and multivariate relationships among individual nutrients in soil and seed, and among ratios of C, N, P, and S, as the major nutrients in the nutrition of oilseed crops. In addition, the ability of nutrients in soil and in seed to discriminate among soil series, and the functional relationships between the same nutrients in soil and seed were investigated.

Canonical correlations

Statistically strong multivariate relationships (Canonical R = 0.93; $R^2 = 0.86$; $\chi^2 = 1103$; p = 0.0001) between nutrients in each soil and in Cuphea seed produced on that soil (Fig. 4A) clearly distinguished between soils within and between both cropping seasons. Total redundancy for nutrients in soil (76.6%) was numerically comparable to the one estimated for nutrients in Cuphea seed (75.3%). The respective statistical multivariate relationships for nutrient ratios in soils and seed (Fig. 4B) were also significant (Canonical R = 0.75; $R^2 = 0.57$; $\chi^2 = 75.2$; p = 0.0001), albeit smaller in magnitude and resulted in a smaller level of separation between soils, although Barnes and Barnes-Buse were largely delineated from Hamerly and Parnell. Negative canonical loadings of P:S and N:P in soil and N:S, N:P, and C:N in seed; and positive loadings of C:N, N:S, and C:P in soil, and P:S and C:P in seed, contributed to separating Barnes and Barnes-Buse from Hamerly and Parnell along both canonical axes, with some overlap at the center of Fig. 4B. Total redundancies were larger for nutrients in soils (76.6%) and in seed (75.3%) (Fig. 4A) as compared to smaller values for nutrient ratios in nutrient ratios in soil (46.2%) and in Cuphea seed (38.6%) (Fig. 4B).

Bivariate relationships between nutrient ratios

Correlation coefficients between the same or between different nutrient ratios in soil and seed and their levels of significant (Table 2) averaged over years and soils indicated that almost 50% had significant levels of association. Nutrient ratios containing C (i.e., C:N and C:P) had negative and significant r-values with their counterparts; those containing S had positive and significant r-values with their counterparts, while soil and seed P:S ratios had the strongest association (r = 0.79; $p<0.001$). The N:P was an exception. Similarly, soil C:N and C:P were more interactive significantly with nutrient ratios in seed than the remaining nutrient ratios. The r-values displayed different patterns in response to annual variation and the percent of significant associations dropped from 44 to 24% over time. Correlations between the same nutrient ratios in soil and seed displayed either a shift in sign and level of significance (C:N), sign (C:P), magnitude (N:S and P:S), or no change (N:P) over time; while the P:S ratios maintained a large, positive and significant r-values under favorable (r = 0.86; $p<0.001$) and drought conditions (r = 0.78; $p<0.001$). Differences in percent significant correlations between nutrient ratios in Barnes (40%), Barnes-Buse (32%), Hamerly (36%) and Parnell (36%) were relatively small; however, when assessed over soils, C:N ratio in seed had the smallest (10%) percent of significant bivariate correlations with soil nutrient ratios, followed by C:P and N:S (40%, each), N:P (45%), and P:S (50%). Correlations between the same nutrient ratios in soil and seed differed markedly in sign, magnitude and level of significant between soils. The C:N ratios had a negative and significant r-value in Barnes-Buse, C:P displayed negative and significant r-values in all soils, N:P had positive (in Barnes and Hamerly) and negative (in Barnes-Buse and Parnell) none-significant r-values, N:S had positive and significant r-value in Barnes, and P:S had positive and significant r-values in all soils except Barnes-Buse. Soils and seed produced on the same soil differed as to the nutrient which was significantly correlated with and determined the magnitude of each of five nutrient ratio. The C:N ratios in Barnes and Barnes-Buse were correlated with C (r = 0.69; $p<0.05$), but not with N; whereas those in Hamerly and Parnell were negatively correlated with N (r = -0.60 and -0.69; $p<0.05$, respectively) and positively correlated with C (r = 0.78 and 0.83; $p<0.05$, respectively). Soil C in Barnes and Barnes-Buse was positively correlated with C:P (r = 0.98, and 0.94; $p<0.05$, respectively); whereas, correlation coefficients with P were negative, but not significant. The C:P ratios in Hamerly and Parnell, paralleled their C:N ratios, where soil C r-values in both soils were large (r = 0.93; $p<0.05$), while P r-values were negative and significant (r = -0.53, and -0.85; $p<0.05$, respectively). The only significant correlation with soil N:P was with P in Hamerly (r = -0.42; $p<0.05$); whereas, the N:S ratio was negatively and significantly ($p<0.05$) correlated with S, but not with N in Barnes (r = -0.72), Hamerly (r = -0.54) and Parnell (r= -0.59), but not in Barnes-Buse. Finally, the P:S ratio was negatively and significantly ($p<0.05$) correlated with S in Barnes (r = -0.93), Barnes-Buse (r = -0.67), Hamerly (r = -0.88), and Parnell (r = -0.90); and significantly and positively correlated with P in Hamerly (r = 0.53) and Parnell (r = 0.72), but not in Barnes and Barnes-Buse. The respective correlations and dynamics of the same nutrient ratios in seed were substantially different from those in soils.

Table 2. Correlation coefficients and their level of significant (*, *p*<0.05) between nutrient ratios in soil and in seed for the whole data set averaged over years and soils, and for each year and soil series.

Factor	Year/Soil series	Nutrient ratios in Soil	Seed C:N	C:P	N:P	N:S	P:S
All		C:N	-0.24*	-0.39*	-0.36*	-0.32*	0.12
		C:P	-0.19	-0.48*	-0.48*	-0.29*	0.38*
		N:P	0.22	0.11	0.12	0.20	0.26*
		N:S	0.28*	0.13	0.10	0.38*	0.60*
		P:S	0.20	-0.05	-0.06	0.49*	0.79*
Year	2005	C:N	0.21	0.19	0.11	0.40*	0.38*
		C:P	0.56*	0.13	-0.07	-0.71*	0.88*
		N:P	0.21	-0.08	-0.17	0.07	0.21
		N:S	0.36*	-0.09	-0.19	0.40*	0.61*
		P:S	0.38*	0.01	-0.13	0.65*	0.86*
	2006	C:N	-0.36*	0.19	0.22	0.13	0.20
		C:P	-0.43*	-0.15	-0.18	0.29	0.63*
		N:P	0.25	-0.15	-0.16	0.10	0.32
		N:S	0.17	-0.14	-0.14	0.29	0.59*
		P:S	-0.14	-0.15	-0.13	-0.63*	0.78*
Soil	Barnes	C:N	-0.32	-0.53	-0.55*	-0.77*	-0.45
		C:P	-0.37	-0.63*	-0.67*	-0.67*	-0.42
		N:P	0.39	0.43	0.41	0.38	0.33
		N:S	0.34	0.52	0.54*	0.62*	0.62*
		P:S	0.05	0.35	0.45	0.67*	0.77*
	Barnes-Buse	C:N	-0.69*	-0.56*	-0.45	-0.62*	-0.45
		C:P	-0.85*	-0.73*	-0.61*	-0.89*	-0.63*
		N:P	0.14	0.04	-0.11	0.09	0.32
		N:S	0.17	0.08	-0.14	0.17	0.45
		P:S	-0.19	-0.21	-0.20	0.14	0.36
	Hamerly	C:N	-0.27	-0.51*	-0.47*	-0.60*	-0.05
		C:P	-0.19	-0.81*	-0.80*	-0.72*	0.41*
		N:P	0.25	0.12	0.05	0.26	0.29
		N:S	0.31	0.04	0.02	0.21	0.39*
		P:S	0.17	-0.32	-0.34	0.05	0.54*
	Parnell	C:N	0.19	-0.24	-0.27	-0.42	0.13
		C:P	0.11	-0.72*	-0.65*	-0.54	0.59*
		N:P	0.02	-0.54	-0.43	0.04	0.58*
		N:S	0.05	-0.74*	-0.60*	-0.20	0.71*
		P:S	0.04	-0.75*	-0.65*	-0.50	0.57*

The C:N ratio in Barnes-Buse was the only ratio significantly ($p<0.05$) correlated with N (r = -0.89) and C (0.72); while N, but not C, was negatively and significantly ($p<0.05$) correlated with the C:N ratio in Barnes (r = -0.94), Hamerly (r = -0.79), and Parnell (r = -0.93). Barnes and Barnes-Buse displayed similar levels of significance ($p<0.05$) between each of C (r = 0.84 and 0.86, respectively) and P (r = -0.98, and -0.58, respectively) with the C:P ratio; while, P but not C, was significantly correlated ($p<0.05$) with C:P in Hamerly (r = -0.97) and Parnell (r = -0.93). Parnell was the only soil where N was significantly ($p<0.05$) correlated with N:P (r = 0.74); while P was negatively and significantly correlated with N:P in Barnes (r =-0.96), Hamerly (r = -0.96), and Parnell (r = -0.87). The N:S ratio was significantly ($p<0.05$) correlated with N in Barnes-Buse (r = 0.69) and Parnell (r = 0.67); while it was negatively and significantly correlated with S in Barnes (r = -0.97), Barnes-Buse (r = -0.77), Hamerly (r = -0.97), and Parnell (r = -0.65). Finally, the P:S ratio was significantly ($p<0.05$) correlated with P in Parnell (r = 0.84); while it was negatively and significantly correlated with S in Barnes (r = -0.68), Barnes-Buse (r = -0.72), and Parnell (r = -0.79).

Discrimination between soils

Nutrients in soil fully discriminated between all four soils, with 100% correct classification of Barnes, Barnes-Buse, and Parnell, and 93.7% of Hamerly, along canonical discriminant Root1(R^2 = 0.74) and Root2 (R^2 = 0.10) (Fig. 5A). Root1 totally separated Barnes and Barnes-Buse from Hamerly and Parnell; whereas, Root2 separated Barnes from Barnes-Buse. The large level of discrimination along Root1 is attributed to negative loadings of a group of nutrients, including Al, B, Mn, Sr, P, V, Li, Mg, Ni, Be, Cu, and Zn, in decreasing order; and to the positive loadings of another group of nutrients, including Ca, Ti, Na, Cr, Si, Ba, K, and Fe, in increasing order. Hamerly and Parnell are characterized by having larger nutrient contents of the first group; whereas, Barnes and Barnes-Buse of the second. Nutrients in seed had less discriminatory power between soils as compared with nutrients in soils (Fig. 5B). Barnes-Buse was the only soil to be 100% correctly classified, followed, in decreasing order, by Parnell (91.7%), Hamerly (90.6%), and Barnes (78.6%). Only 11 of the 19 nutrients found in soil with positive or negative loadings on Root1 in Fig. 4A were detected in seed and had negative (Al, B, Mn, Ca, Zn, P and Mg, in decreasing order), and positive (K, S, Sr, and Si, in increasing

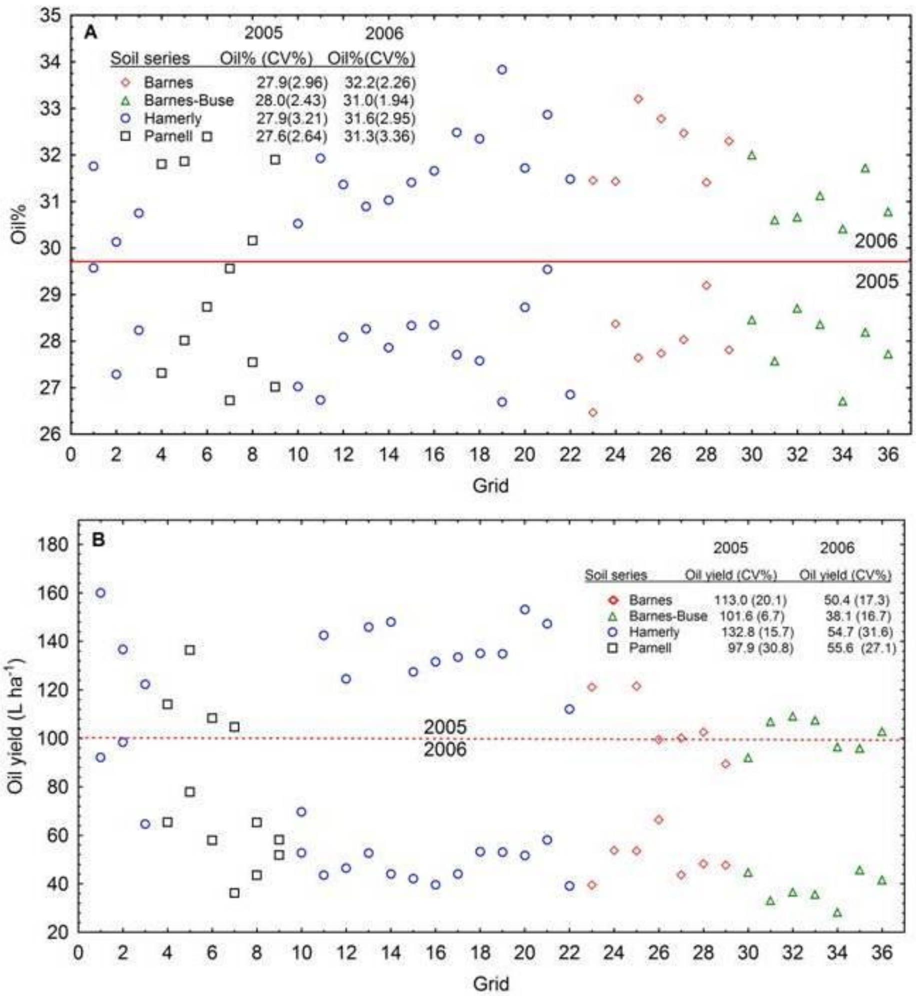

Fig 2. Basic statistics (mean and coefficient of variation, CV%) of oil content (A) and oil yield (B) of Cuphea in four Mollisols and in each of 36 soil grids during two growing seasons.

order) loadings on Root1 and contributed to a large (R^2 = 0.79) level of discrimination between all four soils. Root2 (R^2 = 0.16) contributed to a much smaller level of separation within soils (Fig. 5B). Seven micronutrients found in soils (Ba, Be, Cr, Li, Na, Ti, and V) were not detected in seed and had no discrimination power at the seed level.

Functional relationships among nutrients

The slopes and intercepts in RMA regression analyses were used to express similarities and or differences between nutrients within each soil series and the same nutrient among soil series (Fig. 6A-D). The range of values of both regression coefficients, and coefficients of determination (values next to each nutrient symbol) were large in both cases. A negative and significant relationship was found between slope and intercept in all soils (r-values ranged from -0.72 to -0.85, p <0.0001). Some nutrients exhibited positive relationships between slope and intercept in each soil (e.g., S in all soils; Cu, except in Hamerly); others exhibited different positive and negative combinations in different soils (e.g., Al, Zn). The level of certainty with which the functional relationship were estimated between nutrients in soil and seed (i.e., R^2 values) differed among nutrients and among soils. The R^2 values ranged from 0.04 (Zn) to 0.31 (Si) in Barnes (Fig. 6A); from 0.03 (P) to 0.42 (K) in Barnes-Buse (Fig. 6B); from 0.02 (Zn) to 0.65 (Si) in Hamerly (Fig. 6C); and from 0.04 (P) to 0.49 (Ca) in Parnell (Fig. 6D). A few nutrients had extreme slope and/or intercept values in one or more soils. Three nutrients (Al, Fe and Si) had the most positive slopes and most negative intercepts in Barnes; whereas, Al (in Barnes-Buse) along with Si (in Hamerly) had the most negative slope and positive intercepts. Isometric relationships between soil and seed nutrients comprised a small portion (20.0%), while the majority (80.0%) was allometric. Positive isometric relationships were found for Cu and Mn in Barnes; for Ba and Zn in Barnes-Buse; for B, Mn and Sr in Hamerly; and for Ba, Fe, Mn, and K in Parnell (Fig. 6A-D). Negative isometric relationships were found for K and Zn in Barnes; Al in Barnes-Buse; for Fe, Si and Zn in Hamerly; and for P in Parnell. Coefficients of the reduced major axes describing the functional relationships between nutrient ratios in 2005 and 2006 estimated on soil and seed samples were all significant (Table S1). Four combinations of positive and negative intercepts and slopes, describing this relationship over time, can be identified. The C:N in soil was the only nutrient ratio with negative intercept and negative slope; and had along with P:S in soil and seed had positive intercepts and slopes. The remaining nutrient ratios whether in soil or seed had either negative intercepts and positive slopes (N:P and N:S) or positive intercepts and negative slopes (C:P). Coefficients of determination (R^2) for nutrient ratios in soil ranged from small (0.27 for C:P), to moderate ($0.40 < R^2 < 0.60$ for N:S, N:P, and C:N, in increasing order),

Table 3. Basic statistics (mean and standard deviation, SD) of covariates (soil water, NO_4^+, NO_3^-, ECe, ECa, and pH), level of significance of fixed factors [year and soil series, *p(F)*] and percent variance and its significance [*p(z)*] accounted for by random factors (grid within soil series and year x soil series) in Cuphea performance (seed weight, seed yield, oil content and oil yield) produced on four Mollisols.

Dependent variable	Covariates (soil)						Fixed factors		Random factors			
	Soil water	NO_4^+	NO_3^-	ECe	ECa	pH	Year	Soil	Grid(soil)		Year x Soil	
Mean	18.4	11.9	25.8	43.5	35.8	7.8						
SD	4.5	2.9	13.7	5.9	10.8	0.4						
	p(F)								*p(z)*	%Variance	*p(z)*	%Variance
Seed wt	0.0001	0.0001	0.01	0.52	0.04	0.83	0.03	0.42	0.17	12.7	0.21	27.6
Seed yield	0.0001	0.0001	0.003	0.54	0.02	0.85	0.02	0.45	0.25	7.7	0.23	22.5
Oil (%)	0.0001	0.0001	0.003	0.74	0.16	0.55	0.02	0.72	0.35	5.3	0.09	43.2
Oil yield	0.0001	0.0001	0.02	0.46	0.03	0.91	0.04	0.43	0.17	13.8	0.23	28.8

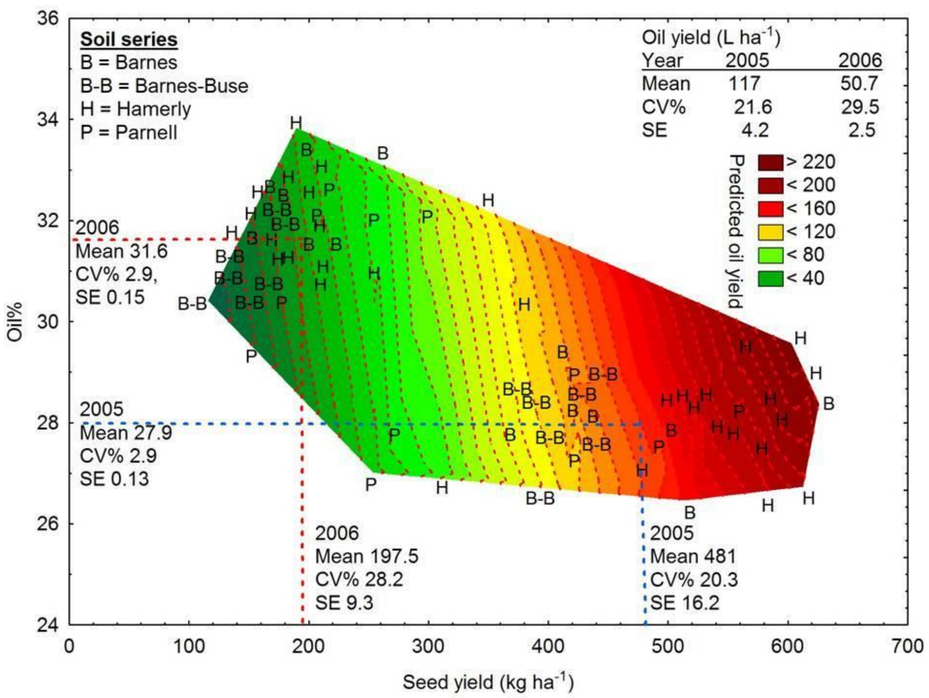

Fig 3. Empirical data derived from statistical analyses of seed yield, oil content and oil yield of Cuphea from four soil series, and predicted oil yield based on spatio-temporal variation in 36 grids in four soil series along two transects and averaged over two cropping seasons.

and reached 0.77 for P:S. The respective nutrient ratios in seed were relatively smaller in magnitude, and R^2 values, except for P:S (R^2 = 0.69), ranged from 0.19 to 0.35 for N:S, C:P, N:P, and C:N, in increasing order. The *t*-test for intercept and slope comparisons between nutrient ratios in soils and in seed indicated that pairs of intercepts and pairs of slopes differed significantly from each other ($p<0.05$), except the intercepts for P:S, and the slopes for N:P.

Assessment of crop performance

Five mixed models, including several combinations of fixed and random factors, with or without two sets of covariates, explained a wide range of variances in crop performance (i.e., seed weight, seed yield, oil content and oil yield) as dependent variables; whereas, three mixed models explained relatively smaller amounts of variation in ratios of four seed nutrients as dependent variables. The inclusion of soil attributes or soil nutrient ratios in both sets of models resulted in changes in the level of significance of fixed factors, and the amount of variance explained by the random factors.

Sources of variation in crop performance

Basic statistics (mean and standard deviation, SD) of Cuphea performance (Table S2), expressed as seed weight (g), yield (kg ha^{-1}), oil content (%), and oil yield (L ha^{-1}) indicated that the variation averaged over soils and years in seed weight (C.V. = 4.0%) and oil content (C.V. = 9.0%) was much smaller than the variation in seed yield (C.V. = 50.0%) and oil yield (C.V. = 51.0%). A mixed model, with years, soils and their interaction, suggested that annual variation and the soil response to that variation had large impact on yield and soil yield, as compared to their impact on seed weight and oil content. The same variables largely responded in the same manner to the random factors in the mixed model. Small portions of total variation were accounted for by differences among grids within soils; whereas, grids within soils responded significantly to differences between years, and this response accounted for significantly larger portions of total variation in all variables, except seed weight. Both random factors accounted for a total of 10.8, 96.0, 69.0, and 95.8% of variation in seed weight, yield, oil content, and oil yield, respectively. A slight change in components of the mixed

Table 4. Basic statistics (mean and standard deviation, SD) of nutrient ratios in soil as covariates (C:N, C:P, N:P, N:S and P:S), level of significance of fixed factors [year and soil series, *p(F)*] and percent variance and its significance [*p(z)*] accounted for by random factors (grid with soil series and year x soil series) in Cuphea performance (seed weight, seed yield, oil content and oil yield) produced on four Mollisols.

Dependent variable	Covariates (nutrient ratios in soil)					Fixed factors		Random factors			
	C:N	C:P	N:P	N:S	P:S	Year	Soil	Grid(soil)		Year x Soil	
Mean	16.6	6.1	4.2	5.9	1.2						
SD	9.6	2.5	1.5	2.4	0.04						
			p(F)					*p(z)*	variance	*p(z)*	variance
Seed wt	0.06	0.25	0.17	0.87	0.09	0.14	0.29	0.43	2.9	0.00	0.00
Seed yield	0.001	0.09	0.69	0.51	0.02	0.007	0.25	0.04	20.9	0.14	41.9
Oil (%)	0.001	0.02	0.05	0.004	0.002	0.01	0.52	0.23	12.5	0.24	22.7
Oil yield	0.001	0.12	0.82	0.29	0.08	0.01	0.26	0.03	26.9	0.14	41.1

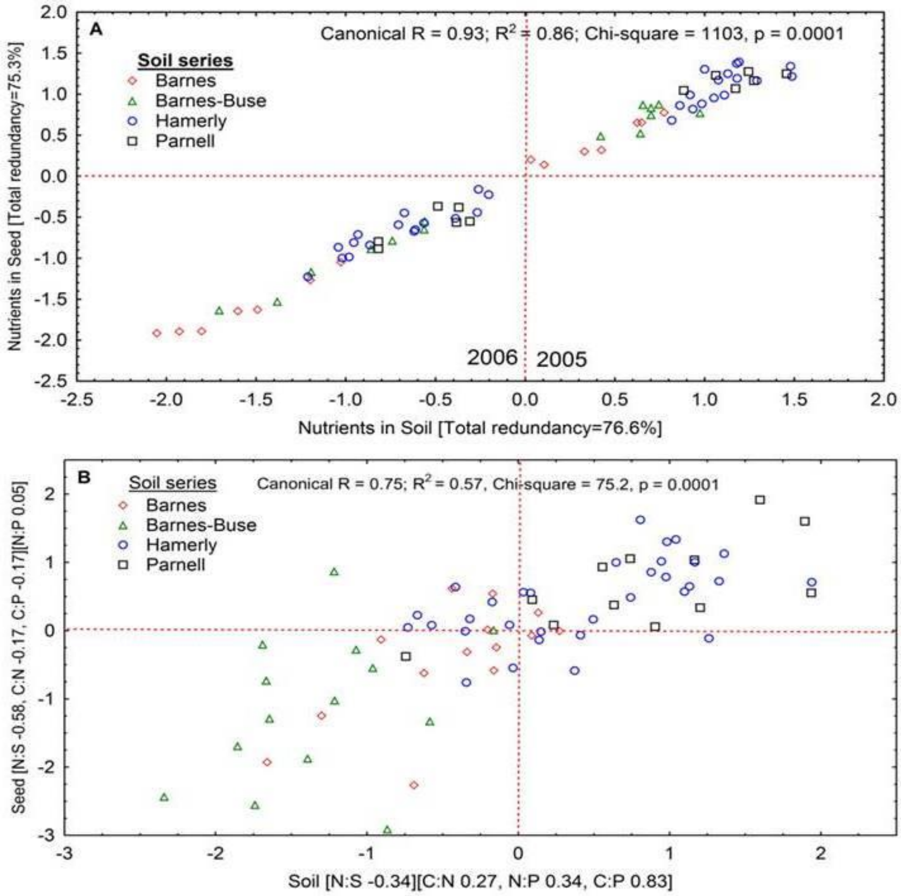

Fig 4. Canonical correlations and their levels of significance between nutrients (A) and between nutrient ratios (B) in four soil series and Cuphea seed produced on those soil series.

model (Table S3) suggested that when the year x soil interaction was used as a random factor, a slight change occurred in the variance explained by year x soil and year x grid(soil) as the random factors in the model. However, total variance accounted for both random factors was 77.2, 93.0, 51.0, and 90.7% in seed weight, yield, oil content, and oil yield, respectively. The inclusion of six soil attributes as covariates in a third iteration of the original mixed model (Table 3) resulted in a major shift in the variance structure due to random factors but not to the significance of fixed factors. The soil attribute exhibited a wide range of variation (expressed as C.V.). Soil reaction (pH) had the smallest (C.V. = 5.0%), followed by ECe (C.V. = 14.0%), then by soil water content and NH_4 (C.V. = 24.0%), ECa (C.V. = 30.0%), and NO_3 (C.V. = 50.0%). The level of significance of these covariates paralleled their level of variation, with ECe and pH having no significant effects on all dependent variables. Both random factors accounted for 40.3, 30.2, 48.5 and 42.6% of total variation in seed weight, seed yield, oil content, and oil yield, respectively. Five soil nutrient ratios were included in the fourth iteration of the original mixed model (Table 4) and their effects on the performance of fixed and random factors were evaluated. The P:S ratio was the only one with negligible variation across soils and years (C.V. = 3.0%); whereas, the remaining ratios exhibited large levels of variation ranging from 36.0% for N:P, to 41.0% for each of C:P and N:S, and a maximum value (59.0%) for C:N. The C:N and P:S ratios, with the largest and smallest

Table 5. Loadings (correlation coefficients, underlined values are not significant; $p>0.05$) of factors and independent variables on the first component in each of nine stepwise PLS regression models and their test statistics for the calibration and validation of oil content and oil yield of Cuphea produced on four Mollisols.

Variable	Loadings of factors and independent variables on the first PLS component																Test statistics		
	Year		Soil series				Nutrient ratios in soil					Nutrient ratios in seed					R^2X	R^2Y	Q^2Y
Model	2005	2006	Barnes	Barnes-Buse	Hamerly	Parnell	C:N	C:P	N:P	N:S	P:S	C:N	C:P	N:P	N:S	P:S			
Oil content																			
1	-0.72	0.72	0.0	0.0	0.0	0.0											0.33	0.83	0.79
2			0.24	0.25	-0.15	-0.27	0.70	0.60	-0.42	-0.22	0.22						0.26	0.43	0.21
3			-0.15	-0.25	0.09	0.12						-0.29	-0.57	-0.55	-0.58	-0.15	0.33	0.42	0.37
4							0.71	0.59	-0.41	-0.25	-0.27						0.51	0.42	0.31
5												-0.27	-0.58	-0.55	-0.54	-0.74	0.71	0.42	0.40
6							0.39	0.37	-0.20	-0.16	-0.34	-0.23	-0.47	-0.45	-0.43	-0.61	0.45	0.56	0.53
7	-0.47	0.47	-0.07	-0.05	0.02	0.05						-0.21	-0.45	-0.42	-0.43	-0.52	0.42	0.71	0.63
8	-0.52	0.52	0.05	0.08	-0.04	-0.08	0.46	0.45	-0.21	-0.17	-0.43						0.34	0.75	0.66
9	-0.42	0.42	0.01	0.01	-0.13	-0.02	0.32	0.33	-0.14	-0.12	-0.27	-0.18	-0.38	-0.35	-0.37	-0.35	0.36	0.72	0.68
Oil yield																			
1	0.70	-0.70	-0.08	-0.10	0.15	0.12											0.33	0.79	0.77
2			-0.15	-0.45	0.39	0.12	-0.59	-0.65	0.25	0.08	0.39						0.29	0.49	0.25
3			0.09	0.0	0.15	-0.22						0.20	0.61	0.59	0.52	0.08	0.31	0.43	0.35
4							-0.71	-0.70	0.29	0.11	0.24						0.47	0.52	0.36
5												0.24	0.59	0.57	0.54	0.54	0.71	0.38	0.38
6							-0.40	-0.42	0.15	0.11	0.52	0.21	0.49	0.47	0.43	0.65	0.44	0.59	0.52
7	0.47	-0.47	0.01	0.01	0.04	-0.08						0.19	0.45	0.44	0.42	0.53	0.42	0.66	0.58
8	0.55	-0.55	-0.03	-0.12	0.14	-0.05	-0.38	-0.48	0.04	0.03	-0.27						0.34	0.75	0.67
9	0.42	-0.42	-0.02	-0.05	0.07	-0.02	-0.32	-0.36	0.11	0.07	0.31	0.16	0.38	0.37	0.34	0.42	0.36	0.71	0.67

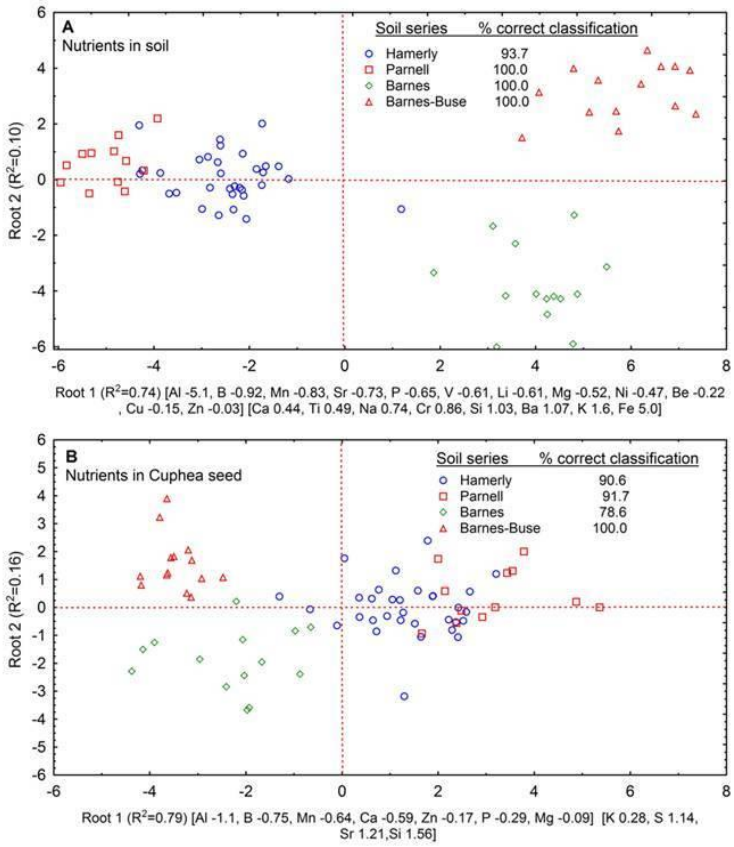

Fig 5. Discriminant analyses between four soil series and based on nutrients in soils (A) and nutrients in Cuphea seed (B) produced on those soils and quantified by percent correct classification, loadings of nutrients on the first (Root 1) and second (Root 2) canonical roots and the amount of variance (R^2) accounted for by these roots.

variation, respectively, had significant effects on all independent variables; oil content was affected by all nutrient ratios; whereas, the effects of C:P on seed weight and oil yield; and the effects of N:P and N:S on all variables, except oil content, were not significant. Significance levels for fixed factors were similar to those in the original mixed model; whereas, only grids within soils, as a random factor, accounted for significant amount of variation in yield and oil yield. Nevertheless, the total amount of variation accounted for by both random factors was small (35.2%) in oil content, and reasonably large in yield (62.0%), and oil yield (68.0%), but none in seed weight. Variation levels in the respective nutrient ratios in Cuphea seed, when used as covariates in the sixth iteration of the original mixed model (Table S4), were extremely small as compared with those in soil. The P:S (0.08%) and C:N (2.0%) were the least variable; C:P and N:P (9.0%) were intermediate, and N:S was the largest (11.0%). The majority (65%) of the p(F) values of the nutrient ratios were significant; however, none of these nutrient ratios had a significant effect on seed weight; N:S had no significant effects on yield and oil yield. The variance structure, as affected by fixed and random factors, was similar to the original model, with annual variation having significant effects on all dependent variables; therefore, relatively small amount of total variation were accounted for by the random factors in seed weight (10.2%), yield (45.7%), oil content (31.1%, and oil yield (39.3%).

Sources of variation in seed nutrients

Five nutrient ratios in Cuphea seed, when used as dependent variables (Table S5), exhibited a wide range of response to fixed and random factors. Annual variation exerted significant effects on all nutrient ratios; whereas, soils and their interaction with years had significant effects on all ratios, except C:N and C:P, respectively. Random factors accounted for non-significant amounts of variation in C:P, N:P, and N:S; grids within soils accounted for significant amount of variation in C:N (71.2%) and P:S (25.9%); whereas their interaction with annual variation accounted for an additional 43.5% of variation in P:S. The remaining total variation estimates were not significant. The inclusion of soil attributes (Table S6) in the mixed model restructured the results of the analyses of variance and the variance components estimates. Nutrient ratios in seed exhibited significant responses to most (67.0%) soil attributes. None of the covariates had a significant effect on C:N; additionally, soil water content had no significant effects on N:S and P:S, while pH did not affect C:P and N:P. Except for the annual variation as a fixed factor, which had significant effects on all dependent variables, none of the remaining factors, whether fixed or random, had a significant effect or accounted for an appreciable amount of variance in the dependent variables. Similarly, when nutrient ratios in soil were introduced as covariates in the mixed model, they triggered further restructuring of the analyses of variance and variance components analyses (Table S7) of the original mixed model presented in Table S5. Almost 50% of the covariate effects were significant; C:N in seed was not significantly affected by any of the covariates; and not a single nutrient ratio in soils had a significant effect on its counterpart in seed, except P:S. The effects of fixed and random factors were similar to those in the previous iteration of the mixed model; however,

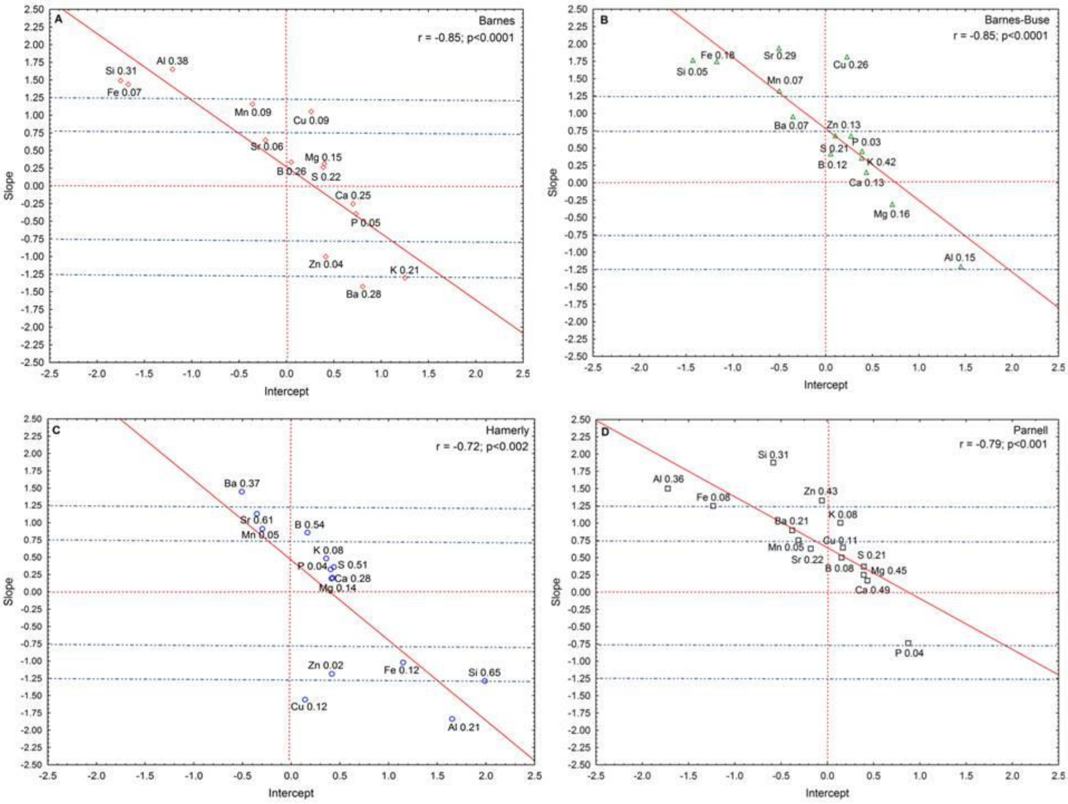

Fig 6. Functional relationships (quantified by a slope and intercept of reduced major axes) and amount of variance explained (R2, following nutrient symbols) for nutrients estimated in soil samples of Barnes (A), Barnes-Buse (B), Hamerly (C), and Parnell (D) soil series and Cuphea seed produced on these soil series.

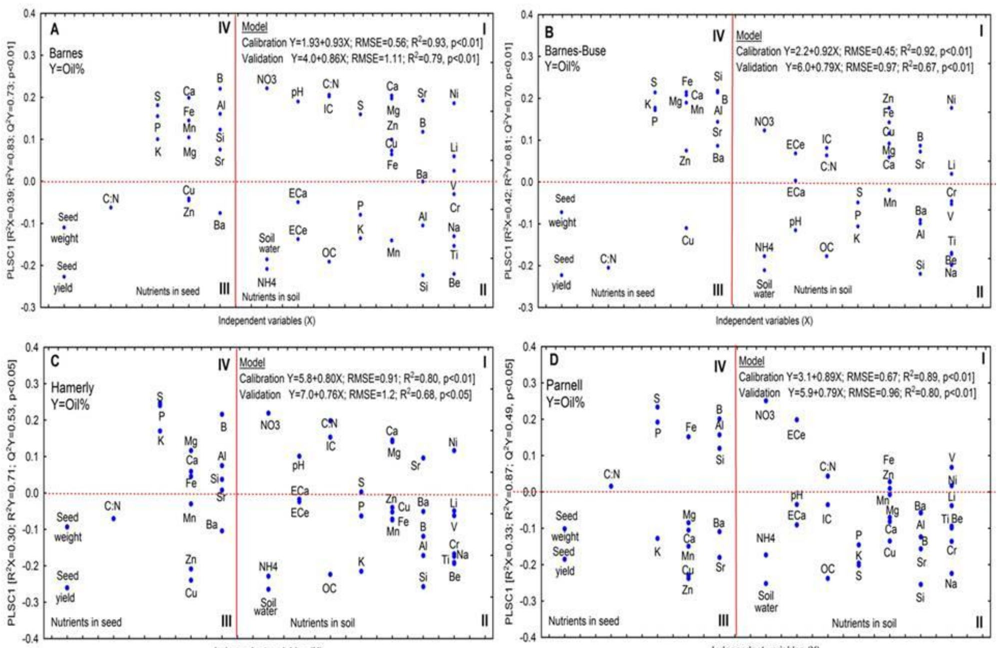

Fig 7. Partial least squares regression models and their test statistics for oil content in Cuphea seed produced on Barnes (A), Barnes-Buse (B), Hamerly (C), and Parnell (D) soil series as function of soil variables, and nutrients in soil and Cuphea seed.

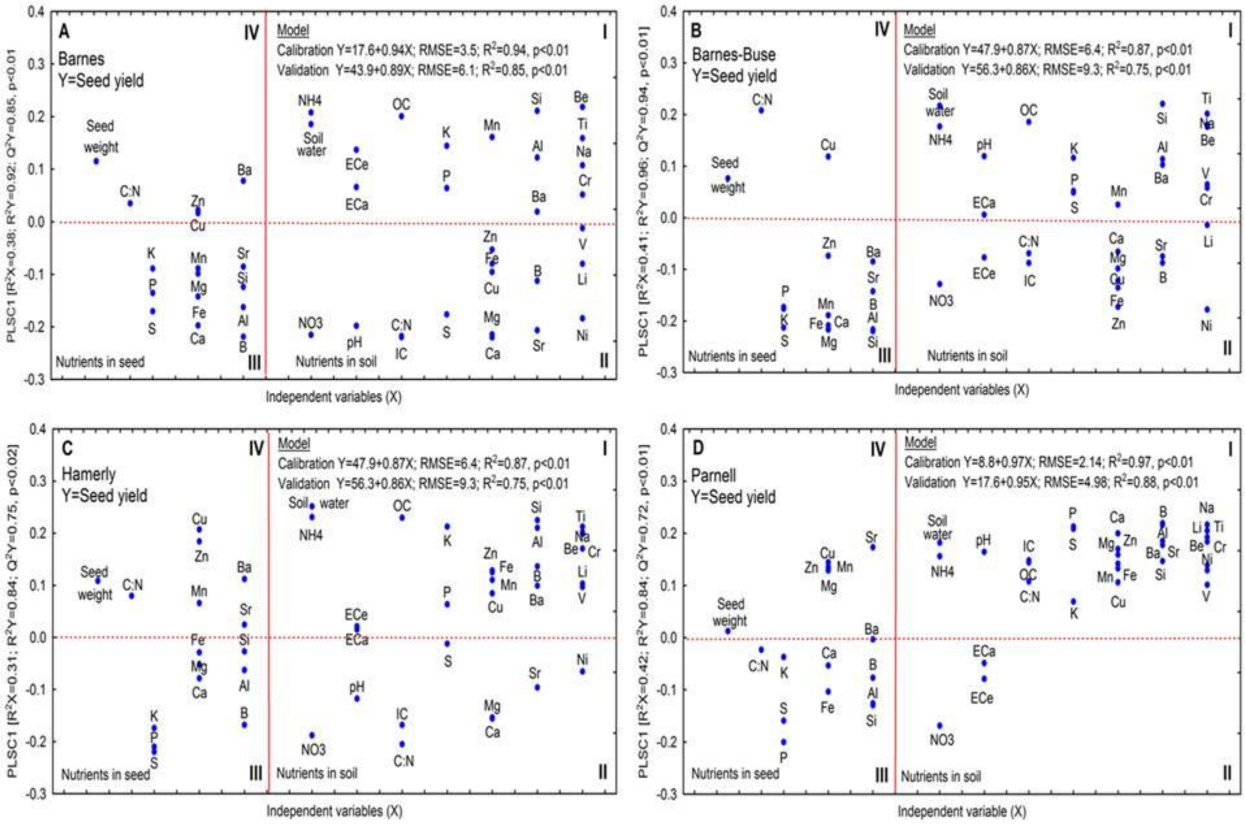

Fig 8. Partial least squares regression models and their test statistics for Cuphea seed yield produced on Barnes (A), Barnes-Buse (B), Hamerly (C), and Parnell (D) soil series as function of soil variables, and nutrients in soil and Cuphea seed.

a larger, although not significant (50.5%) portion of total variation in C:N was explained by both random factors.

Empirical modeling of crop performance

Calibration and validation PLS regression models provided detailed quantitative and graphical statistical information on oil content (Fig. 7A-D) and oil yield (Fig. 8A-D). The validation models in each case provided enough quantitative data to further develop calibration and validation models using the first principal component in each case and to assess the reliability of the newly developed PCA models.

Empirical modeling of oil content.

Four PLS regression models (Fig. 7A-D) described the amount of variation extracted from independent variables comprising soil attributes, soil micro- and macro-nutrients, two seed variables (seed weight and seed yield), and micro- and macro-nutrients in seed (R^2X; ranged from 0.30 in Hamerly to 0.42 in Barnes-Buse), calibration coefficient of determination (R^2Y; ranged from 0.71 in Hamerly to 0.87 in Parnell), and validation coefficient of determination (Q2Y; ranged from 0.49 in Parnell to 0.73 in Barnes). There were some similarities and large differences between soil series in loadings of independent variables on the PLSC1 (i.e., correlation coefficients between an independent variable and PLSC1). Soil attributes (i.e., ECa, ECe, pH, soil water content) displayed different loadings and associations (e.g., ECa and ECe in Hamerly; Fig. 7C); while soil water content had negative loadings in all soil series. The C- and N-related variables in soil (i.e., C:N, IC, OC, NH_4^+ and NO_3^-) displayed a wide range of loadings and associations. Loadings of C:N and its association with IC, for example, were larger in Barnes and Hamerly (Fig. 7A and 7C, respectively), than in Barnes-Buse and Parnell; and the antagonistic effects on oil content of C:N and IC, as a group, and OC, were larger in Barnes and Hamerly as compared with their effects in Barnes-Buse and Parnell. A group of seven micro-nutrients (Be, Cr, Li, Na, Ni, Ti, and V) in soil had positive and negative loadings and impacted oil content, but were not detected in the seed. A second group of nutrients in soil and seed (Ca, Cu, Fe, Mg, Mn, and Zn) contributed to oil content determination and exhibited slightly different loadings on PLSC1 in different soils. Three soil macro-nutrients (i.e., K, P, and S) displayed similar loading patterns in all soils except S in Barnes and Parnell. Loadings of seed nutrients, except those which were not translocated to, or detected in seed, had loadings similar in sign, but not necessarily in magnitude, to their counterparts in soils; however, with a few exceptions (e.g., S in Barnes-Buse and Parnell; Mn in all soils; and P and K in all soils except Parnell, where there was a disassociation between loadings of these two nutrients in seed). The largest negative loading of C:N was found in Barnes-Buse where it was strongly associated with grain yield, while it had zero (in Parnell) or slightly negative loadings on PLSC1 (in Barnes and Hamerly), while its association with seed yield was not strong. Finally, seed yield and, to a lesser extent, seed weight invariably had negative loadings on PLSC1 in all soils. Calibration and validation models based on PCA resulted in accounting for large and significant portions of variation (R^2) in oil content in all soils. Calibration models accounted for

0.80 to 0.93; whereas, validation models accounted for 0.67 to 0.80 of variation in oil contents; the smallest difference between calibration and validation model R^2 estimates (0.09) was in Parnell, followed by Hamerly (0.12), Barnes (0.14), and Barnes-Buse (0.25). The difference in RMSE estimates between calibration and validation models was largest in Barnes (0.55) and Barnes-Buse (0.52), and smallest (0.29) in Hamerly and Parnell; nevertheless, all PCA models were significant (p<0.01).

Empirical modeling of oil yield

The performance of PLS regression models in estimating seed yield in different soil series was comparable to that in estimating oil content; however, with major shifts in variable loadings on and associations with PLSC1. Four PLS regression models (Fig. 8A-D) described the amount of variation extracted from independent variables comprising soil attributes, soil micro- and macro-nutrients, one seed variable (seed weight), and micro- and macro-nutrients in seed (R^2X; ranged from 0.31 in Hamerly to 0.42 in Parnell), calibration coefficient of determination (R^2Y; ranged from 0.84 in each of Hamerly and Parnell to 0.96 in Barnes-Buse), and validation coefficient of determination (Q2Y; ranged from 0.72 in Parnell to 0.94 in Barnes-Buse). In general, loadings of groups of soil attributes and soil and seed nutrients on PLSC1 comprised a mirror image of their loadings on PLSC1 for oil content (Fig. 7A-D). Parnell was the only soil series that differed from others and were variable loadings weren't a mirror image of those in Fig. 7D. Calibration and validation coefficients of determination (R^2) in PC models in different soils ranged from 0.87 to 0.97 and from 0.75 to 0.88, respectively; and the differences between calibration and validation R^2 values were small (0.09 to 0.12). Similarly, the differences between RMSE estimates for calibration and validation PC models in different soils were small and comparable (2.6 to 2.9).

Calibration and validation models for oil content and oil yield

Loadings of factors and independent variables on PLSC1 (Table 5) explained a wide range of variation in oil content and oil yield. Temporal (i.e., years), spatial (i.e, soil series), nutrient ratios in soil and in seed were introduced in a stepwise manner in PLS regression models to predict oil content and oil yield in Cuphea. All models resulted in explaining significant amount of variation at the validation stage of model building (p<0.05), except Model 2 for both dependent variables. Temporal variation and soil series explained 0.79 and 0.77 of oil content and oil yield at the validation stage of model building (Model 1, in both cases); whereas soil series, even when nutrient ratios in soil were included, explained non-significant portions in oil content (0.21) and oil yield (0.25). A slight increase in validation variance was achieved when nutrient ratios in seed was included; whereby 0.37 and 0.35 of variation in oil content and oil yield, respectively, were explained at the validation stage of model building (Model 3). The amount of variation extracted from independent variables differed among models and ranged from 0.26 in Model 2 to 0.71 in Model 2; whereas, the amount of variation explained in oil content and oil yield increased gradually from 0.42 (oil content, Models 3, 4, and 5) and from 0.38 (oil yield, Model 5) to 0.83 and 0.79, respectively (Model 1). On the other hand and with the exception of Model 1, the amount of variation in validation variance increased steadily due to the inclusion of additional independent factors (from Model 2 to Model 9) for both dependent variables. Notably, soil series did not contribute significantly to explaining any significant variation in oil content or oil yield in the presence of the strong effects of temporal variation (Models 1, 7-9). The difference between R^2Y and Q^2Y, which reflects the reliability of the validation model, was the largest for soil series and soil nutrient ratios (Model 2), and smallest for nutrient ratios in seed (Model 5). Most (78%) of the nutrient ratios in soil across all models had significant loadings on PLSC1; while nutrients in seed accounted for >50% of total variation that was explained by the final validation models (68% in oil content, and 67% in oil yield).

Discussion

Extensive and intensive land-use for row-crop production in the Midwestern USA during the last ~150 years resulted in major changes in native soil properties of the Mollisols, including their primary taxonomic feature, i.e., the thick, dark epipedon, mainly due to soil erosion (Soil Survey Staff, 2006). Current and projected demand for oilseed production may accelerate this trend and the new oilseed crops, depending on their relative economic performances, may have to compete for fertile agricultural land with row crops (Nad et al., 2001; Sarda et al., 2013), or be confined to marginal soils with lower native fertility (dos Santos et al., 2013; Olama et al., 2013), especially in developing countries (Olama et al., 2013; Rastgou et al., 2013). The importance of Cuphea oil, as well as oil from several other oilseed crops(Berti and Johnason, 2008), is growing as a source for medium-chain fatty acids, such as caprylic, capric, and merystic, and as potential sources of bioenergy and other industrial products (Kim et al., 2011). Increased demand for these fatty acids is in line with greater use of vegetable oils for industrial purposes which increased by about 50% during the past decade (Haslam and Michaelson, 2013). Therefore, large seed oil content and quality are major objectives of oilseed crop breeders, agronomists and producers (Olama et al., 2013; Wysocki et al., 2013). Earlier (Jaradat and Rinke, 2009), we contended that understanding the homeostatic mechanisms that delineate nutrient accumulation and remobilization in the Cuphea PSR23, their dynamics, and interrelationships would help toward its development as a competitive oilseed crop. The production potential of newly developed oilseed crops such as Cuphea depends, among other factors, on natural soil fertility and rates of fertilizer application. We evaluated the effects of annual and inherent soil variation on the performance of Cuphea grown on four soil series during two contrasting cropping seasons. The annual variation had the largest effects on crop performance, followed by variation within soil series, especially on seed yield, oil yield and oil content, in decreasing order.

Assessment of soil spatial variability

Soil variability is caused by the combined effects of natural processes and management practices, both of which act at different spatio-temporal scales (Castrignanò et al., 2000; Huth and Poulton, 2007; Jaradat and Weyers, 2011). Some of these properties were found to be regionalized (ECe, Fig. 1A and pH, Fig. 1B); others were randomly distributed without a common pattern (e.g., most nutrients in soil, Fig. 5A). Spatial differences in soil properties frequently cause yield variation even in areas apparently considered homogenous (Hakojärvi et al., 2013). Even most soil properties measured or estimated in this and other studies (Shattar and McBratney, 1999;

Korsaeth, 2005; Bayer et al., 2012; Castrignanò et al., 2013) varied spatially, only a few were responsible for variation in crop yield. Nevertheless, farmers may not be able to manage spatial variation in the presence of temporal variation. However, they should be able to predict this variation and minimize its impact on crop yield by using the right management practices at the right time (Jaradat and Weyers, 2011). Regardless of similarities in soil texture, differences among and within soils were significant for a large number of soil attributes, nutrient contents and nutrient ratios (Table 1) suggesting the existence of numerous factors contributing to differences among and within soils. Several forms of N and C (particularly NO_3-N and OC) displayed highly significant differences among and within soils (Table 1), contributed to soil spatial variation, and along with IC, exhibited a wide range of associations with other soil attributes, especially EM_H and EM_V (Fig. 1B). Strong and positive correlation have been reported between ECa and OC (Korsaeth, 2005); however, we obtained significant positive and negative, and non-significant correlations between these variables in different soils, although the overall r-values between OC and each of EM_H ($r = 0.73$; $p<0.05$) and EM_V ($r = 0.81$; $p<0.05$) were positive and significant, (Fig. 1B). Whereas; both N-forms, in addition to soil water, as covariates in mixed model (Table 3) had the strongest effects on crop performance. Although a few significant differences were found between soils for ECa and ECe, the former, which reflects the depth-weighted summarized effect of all factors influencing electrical conductivity in soil (Corwin and Lesch 2005, Korsaeth 2005, Huth and Poulton 2007), is a function of soil texture, cation exchange capacity (CEC) and water content. Also, ECa, but not ECe, as covariates (Table 3) had stronger effects on the crop performance. Moderate ($r = |<0.50|$) correlations between ECe and each of EM_H and EM_V were negative (e.g., Barnes), positive (e.g., Hamerly and Parnell) or 0.0 (e.g., Barnes and Barnes-Buse) (Fig. 1A). Strong correlations between these soil attributes are unlikely to obtain due to effects of moisture contents (i.e., differences between soil *in situ* and the soil extract prepared for ECe) and because EM-38 measurements represent a much deeper horizon than that of soil samples (Corwin, and Lesch). The use of weighted ECa estimates (α_V and α_H) to account for the relative contribution to the signal from the top soil, which was larger for EM_H than for EM_V, improved ECa's performance in accounting for large variance in crop performance using mixed models (Table 3). Soil pH played a stronger role than ECa or ECe in characterizing spatial variation of these soils (Table 1) and along with soil moisture may have affected nutrient use efficiency (Baligar et al., 2001); however, its regionalized distribution and highly variable correlations with ECa and ECe (Fig. 1A) may have rendered it ineffective in explaining any significant variation in crop performance (Table 3). Soil nutrient analyses suggested that the four Mollisols in this and in previous studies at the same (Jaradat and Rinke, 2009) or different locations in the upper Midwest (Kim et al., 2011) and in other agricultural soils around the world (Baligar et al., 2001) are deficient in one or more of the essential nutrients needed to support productive oilseed crop plants. Worldwide elemental deficiencies in macro- and micronutrients for oilseed crops have been reported for Cu, Fe, Mn, S, and Se (Jackson, 2000; Gupta and Gupta, 2005; Ciampitti and Vyn, 2013a; Ciampitti et al., 2013). Deficiencies in Mn, P, Cu and Zn have been reported in Mollisols, including all four soil series used in this study (Jaradat and Rinke, 2009; Jaradat, 2012). Cuphea may experience Mn (and Zn) deficiency in the upper Midwest; this deficiency is a significant global problem under a wide range of environmental and edaphic (e.g., pH) conditions (Hitsuda et al., 2004), and is usually associated with larger available soil-N (Ma and Dwyer, 1999; Olama et al., 2013; Rastgou et al., 2013; Solis et al., 2013), which is a normal practice in row crop production (Dobermann and Cassman, 2002; van Noordwijk and Cadesch, 2002). The impact of pH on Mn contents can be explained on the basis of its association with Hamerly and Parnell (pH>7.5), and not with the calcareous Barnes and Barnes-Buse soils (pH<7.5) (Fig. 1B) as evidenced by its loading on the first discriminant canonical root (Fig. 5A).In addition, these differences were manifested at the level of functional relationships of Mn in Barnes and Barnes-Buse, with slopes of 1.2 and 1.3, respectively (Fig. 6A and B), as opposed to the smaller slope of ~0.8 for Hamerly and Parnell (Fig. 6C and 6D). Adequate, if not large, seed P content can improve plant establishment and increase yields, presumably due to faster initial root growth, which gives seedlings earlier access to growth-limiting resources, such as water and micronutrients (White and Veneklaas, 2012). Phosphorus was significantly correlated with a large number of nutrients, including K, Mg, Ca, Cu, Fe, Zn, in cereals (Nad et al., 2001), legumes (Munier-Jolain and Salon, 2005), and oilseed crops (Yang et al., 2009; Solis et al., 2013; Wysocki et al., 2013), including Cuphea (Berti and Johnson, 2008; Jaradat, 2012). Within-soil variation in P was the smallest among nutrients used in exploring effect of nutrient ratios (i.e., C > N > S > P; Table 1) on crop performance; however, its role in achieving significant correlations with nutrient ratios in seed increased from 40% (with C), to 45% (with N) and 50% (with S) (Table 2) as its ratio with the respective nutrients decreased from, 6.1, to 5.9, and 1.2 (Table 4) suggesting a stronger P nutritional role in conjunction with S than with N or C.

Spatial variation in crop performance

Temporal variation in crop performance was significant and contributed to spatial variation in seed yield and oil yield among and within soils. However, contrary to earlier findings (Ngezimana 2012), the latter was exceptionally small for oil content (Fig. 2A) within years (C.V.% 1.94 to 3.36%) as compared to its variation among years (~15.3%) (Fig. 2A) or compared with exceptionally wide range of CV% values for oil yield within (6.7 to 31.6%) and among years (~63.0%) (Fig. 2B); oil yield was largely a function of seed yield (Fig. 2) rather than oil content (Nad et al., 2001; Kim et al., 2011; Rogerio et al., 2013). Spatial variation in crop performance was quantified by the maximum portions of variation in crop performance explained by the interaction between annual variation and the within soil variation (i.e., year x grids within soils), regardless of the fixed factors (Tables S2 and S3), or covariates (Tables 3 and 4) used in mixed models. The significance of covariates, as a consequence of their spatial variation was illustrated by the non-significant portion of variation attributed to the interaction. Variability in allocation of different nutrients to seeds, as quantified by RMA model parameters (Fig. 6), nutrient ratios (Table 1) and associations between these ratios (Table 2), may be attributed to Cuphea's allometric growth (Niklas, 2006); however, deviations from allometric trajectories can be explained by differences in seed competition for nutrients, for example, within Cuphea capsules (Jaradat and Rinke, 2009; Jaradat, 2012), corn ears (Ciampitti and Vyn, 2013b), wheat spikes (Nad et al., 2001) and legume pods (Munier-Jolain and Salon, 2005). Whereas variation in seed mass may explain most variation in C and N allocation in Cuphea (Jaradat, 2012), a significant portion of the variation in S and P allocation remains unexplained and needs further research in this and other oilseed crops (Grant et al., 2012; Malhi, 2012; Rogerio et al., 2013). The spatial variation in crop performance may depend in large part on nutrient use efficiency which is a function of soil's capacity to supply adequate levels of nutrients, and the ability of crop plants to obtain, transport and remobilize to the developing seed (Baligar et al., 2001; Ciampitti and Vyn, 2013b). The slope (*b*) in RMA analyses may serve as indicator of this efficiency and describe to a large extent spatial variation in crop performance. This parameter (*b*) describes how steep is the relationship between a particular nutrient or nutrient ratio in soil and seed (Niklas, 2006). The isometric and negative slope of Fe, for example, (e.g., Fig. 6C) is an indication of higher efficiency in extracting and storing Fe in Cuphea seed produced on Hamerly as compared to the remaining three soils (e.g., Fig. 6A, B, and D). This conclusion is supported by results presented in Fig. 4A, where Fe had the largest canonical coefficient separating Hamerly (and Parnell) from the other two soils; and in Fig. 7, where Fe loaded negatively in Hamerly and positively in Cuphea seed produced on that soil; both were mirror images of its loadings in the remaining soils. Low nutrient contents of the soil or restricted uptake under conditions of water limitation may have resulted in lower nutrient contents in oilseed crops (Ronnenberg and Wesche, 2010). This phenomenon was demonstrated by canonical correlation analysis of nutrients (Fig. 4A) and nutrient ratios (Fig. 4B), both of which were associated with (Fig. 7 and 8) or explained significant portion of variation in crop performance, whether alone (Table S2) or in combination with other soil attributes (Table S3).

Soil variation vs. nutrients variation and associations

Although the elemental composition of a given plant is species-specific (Zembala et al., 2010), the nutrient content of its seeds depends on environmental, soil, and genetic factors and their interaction (Ciampitti and Vyn, 2013a,b; Ding et al., 2013). Associations between nutrients and between nutrient ratios were demonstrated and quantified by several statistics, including product moment correlations (Table 2), canonical correlations (Fig. 4 and 5), slopes and intercepts of RMA models (Fig. 6), and partial least square regression coefficients or loadings (Fig. 7 and 8); each furnished a portion of a joint spatio-temporal map of soil attributes, nutrients, and crop performance. In spite of planting Cuphea after uniformly-managed and fertilized soybean in 2005 and wheat in 2006 and after uniform fertilizer application to the Cuphea crop in both years, spatial variation (and temporal variation) in soil nutrients persisted. This persistence suggested that native fertility and, presumably, other components of the spatial variation (Fig. 1) were most likely caused by non-manageable factors (Ma et al., 1999; Castrignanò et al., 2000; Koide and Peoples, 2012). Differences between total redundancies in nutrient (Fig. 4A) and nutrient ratios (Fig. 4B) suggested that the first is more powerful than the second in describing nutrient associations. Redundancy in nutrients indicated that ~75% of variation in soil or seed nutrients can be explained by variation in the other set of nutrients; while the respective values for soil (46.2%) and seed (38.6%) nutrient ratios, were much smaller. The drop in the canonical correlation from 0.93 for nutrients to 0.75 for nutrient ratios (Fig. 4) could be attributed to the different nutrient dynamics quantified by model parameters in different soils (Fig. 6), and to differences between nutrient loadings on PLSC1 (Fig. 7 and 8), which separated the nutrients into five groups. The first group was composed of Al, P, S, and Zn, with mixed loadings on PLSC1 of soil nutrients and positive loadings on PLSC1 of seed nutrients. The second was composed of Ba, Ca, K, Mg, Mn, and Sr, with mixed loadings on both PLSC1.The third (B and Fe) had positive loadings on both PLSC1s; while Si and Cu had mixed, but opposite loadings, comprised the last two groups. Total nutrient concentrations in soil do not usually reflect their bioavailability to crop plants in the presence of large spatial variation (Cornu et al., 2007); however, it was possible to quantitatively resolve this issue when the variability within a single soil type was taken into consideration (Fig. 6). Seed reserves of macro- and micronutrients are essential for the first phase of seedling development; therefore, nutrients in Cuphea seed may constitute a significant source of several essential elements necessary to enhance its germination and early seedling growth (Gupta and Gupta, 2005; Jaradat and Rinke, 2009; Jaradat, 2012), both of which are impacted by environmental and edaphic factors in the Midwest. Notwithstanding the importance of carbon skeleton in plant biology, the relationships between C, N, P, and S influence seed yield and oil content of several oilseed crops, including canola (*Brassica napus* L. var *napus*) (Jackson, 2000), sunflower (*Helianthus annuus* L.) (Sheoran et al., 2013), sesame (*Sesamum indicum* L) and safflower (*Carthamus tinctorius* L.) (Rastgou et al., 2013). On the other hand, soil K reserves in these Mollisols are generally large (Jaradat and Weyers, 2011; Wang et al., 2011; Veenstra and Burras, 2012); their association with NH_4-N (Fig. 7 and 8) may indicates potassium ability to enhance N uptake and assimilation in oilseed crops (Romheld and Kirby, 2010; Zhang et al., 2010; dos Santos et al., 2013). Fertilizer applications may cause significant changes in nutrient ratios (e.g., 20% in C:N and 30% in N:P) (Ronnenberg and Wesche, 2010); however, in spite of uniform fertilizer applications, large variation levels were found among and within soils for most ratios of C, N, P, and S in this study. Traditional fertilizer applications in Midwestern USA apply P and K along with N, but this is not always the case for S (Jackson, 2000; Grant et al., 2012; Malhi, 2012); the reserves of which have been depleted due to reduced soil deposition from S atmospheric pollution by about 85% in the last three decades (Sarda et al., 2013). A wide range of nutrient ratios was reported in several crops (Elser et al., 2010), including Cuphea (Jaradat and Rinke, 2009), which indicates the relative importance of one nutrient vs. another (Ronnenberg and Wesche, 2010), and reflects the effects of adjustment to local growth conditions, including environmental, soil and plant nutrition factors (Elser et al., 2010; Obeso, 2010). When averaged over soils, nutrient ratios in soils displayed large levels of variation (C.V. ranged from 36.0 for N:P to 58% for C:N), with one exception (P:S with 3.3%). The respective levels of variation for nutrient ratios in seed were much smaller and ranged from 2.0% for C:N to 11.5% for N:S; whereas, variation in P:S ratio across seed samples was negligible. Apart from difference in variation within soils and seed, the closely similar, albeit large C:N ratios in soils (16.6±9.6) and seed (17.0±0.37) suggested that Cuphea managed to maintain more stable C:N in the sink (i.e., seed) compared to the largely variable ratio in the source (i.e., soil), with N presumed to be the determining nutrient (Chen et al., 2010; Elser et al., 2010; Fujita et al., 2010). The large soil C:N-ratios in this study differed substantially from those reported earlier (Ronnenberg and Wesche, 2010) indicating that C:N ratios in soil are very narrow (8.7± 0.13 to 8.9± 0.19); these differences may be attributed to N-fertilizer sources and management, and to the presence of different and variable forms of N in different soils (Ciampitti and Vyn, 2013a; Wysocki et al., 2013). Larger nutrient ratios in seed as compared to soil found for C:P (12.2 vs. 6.1), N:P (7.1 vs. 4.2), and N:S (12.2 vs. 5.9) as compared with a stable P:S ratio in soils and seed (1.2) suggested that the second nutrient in each ratio (except in P:S, where both nutrients are potentially limiting) was the limiting nutrient in seed. This conclusion is functionally supported by the strongest positive ($r = 0.86$; $p<0.05$) correlation coefficient between P:S in soil and in seed averaged over years and soil series (Table 2). The availability of soil N and P influences their N:P supply ratio, which was found to change over time in Cuphea (Jaradat, 2012) and other oilseed crops (Fujita et al., 2010); whereas, a balanced and stable N:P ratio in plant tissues plays a vital role in plant biology for obvious biochemical reasons (Niklas, 2006; Zhang et al., 2010; Ding et al., 2012), the most important of which is P allocation which represents the capacity to produce proteins (White and Veneklaas, 2012; Rogerio et al., 2013). The increase in N:P ratio from 4.2 in soil to 7.1 in seed was associated with a larger reduction in its level of variation (from 36.0 to 8.8%) and resulted in a more stable ratio in the sink which is largely attributed to N rather than P availability. Ontogenically, N:P ratios in reproductive and metabolic tissues of Cuphea were least variable and were mainly affected by allometric leaf mass and relative growth rate (Jaradat, 2012); both of which are important in determining reproductive allocation in Cuphea and other oilseed crops (Ma et al., 1999; Soils et al., 2013; Ciampitti and Vyn, 2013a; Rastgou et al., 2013). Due to strong linkages between N and S metabolism in plants, N, rather than S availability determine the magnitude of their ratio (Soil et al., 2013; Wysocki et al., 2013) and can be used as a reliable indicator of S deficiency (Grant et al., 2012; Salvagiotti et al., 2012; Wysocki et al., 2013). Generally, seed N:S ratio was closely associated with changes in seed S content rather than changes in seed N (Ciampitt and Vyn, 2013a); however, no consistent relationship with relative seed yield was found in a regional study (Kim et al., 2011). We found a consistent negative and significant relationship between seed N:S ratio and seed S ($r = -0.33$, $p<0.05$), but not with seed N ($r = 0.03$; $p>0.05$), although their respective C.V. values in seed (C.V. = 1.98 and 1.53%) were numerically comparable; while their respective C.V. values in soil (5.4 and 34.5%) were vastly different. On average, N:S ratio was 5.9±2.4 (C.V. = 41.0%) in soils and 12.2±1.4 (C.V. = 11.5%) in Cuphea seed (Table S4); these ratios indicate that source and sink may be S deficient. Cuphea was planted after wheat and soybean, both of which take up large amounts of S (from native fertility sources) for protein and oil synthesis, respectively (Nad et al., 2001). A proportionately narrow N:S ratio (~1:2 to 1:3) was associated with adequately higher seed and oil yield in several oilseed and cereal crops (Nad et al., 2001). Relatively larger soil and seed N:S ratios reported in this study, as covariates, had significant effects on oil content (Table 4 and S4); whereas, N:S ratios in soil and seed had opposite effects on oil content and oil yield associated with a wide range of coefficients in stepwise PLS models (See section: *Empirical Modeling of Crop Performance*, below and Table 5). Finally, soil P but not soil S (Fig. 5A), contributed to full discrimination between soils; whereas, seed P and seed S (Fig. 5B) contributed to large, but not full discrimination between soils. This difference in discriminating power could be attributed to significant differences between soils in P ($p<0.05$), but not in S ($p = 0.5$) (Table 1). Nevertheless, the P:S ratios in soil (1.2±0.04), with no significant differences between soils, ($p = 0.72$; Table 1), and in seed (1.2±0.01) were the narrowest and most stable among all nutrient ratios.

Assessment of crop performance

Interest in low-input oilseed crops, including Cuphea, is rising for industrial use in the upper Midwest because there is limited oilseed acreage, apart from soybean, in this region; in addition, new oilseed crops are needed to diversify the widely-practiced corn-soybean crop rotation (Jaradat and Weyers 2011). Based on its current average (~150 kg ha^{-1}), or maximum (~220 kg ha^{-1}) oil yield reported in this and other studies (Berti and Johnson, 2008; Kim et al., 2011; Solis et al., 2013)], Cuphea may be able to compete, agronomically and economically, with well-established oilseed crops, such as soybean (~360-400 kg oil ha^{-1}) and canola (~400 kg oil ha^{-1}) only if the demand for its specialty oils increases and a price premium is guaranteed. However, oil yield is one of several factors to be considered when selecting an oilseed crop for industrial purposes (Koide and Peoples, 2012). Other considerations may include, but are not limited to, nutrient requirements, the impact on other crops' performance in the crop rotation, and the market value of its oil and derived or byproducts. Seed yield, or any other surrogate variable such as oil yield, oil content, or fatty acid composition, can be measured as end of season static measure of crop performance, but it may not reflect the fluctuations of crop performance throughout the growing season. However, in order to fine-tune resource management and maximize return from areas within a field, insight in crop performance over time was recommended (Dobermann and Cassman, 2002; Grant et al., 2012). To achieve this goal, there is a need to understand soil spatial variability across fields and its influence on crop performance (Shattar and McBratney, 1999; Castrignanò et al., 2000, Corwin and Lesch, 2003; Korsaeth, 2005). We identified pH and ECa, (Fig. 1), soil water content (Fig. 7, 8), soil P:S ratio (Table 5) as important and relevant factors in this regard. Climate and soil factors in Midwestern USA (including locations in IA, MN and ND) caused large fluctuations in Cuphea's seed yield within (114-200%) and among (450%) locations and years (Berti et al., 2007; Kim et al., 2011), but relatively smaller fluctuations in oil content (3.0-4.0%); however, no clear relationship was established between both variables across those experimental sites in the Midwest. Cuphea performance may have been impacted by within (Fig. 2) and among grid variation regardless of fixed factors (Tables S2 and S3) or covariates (Tables 3, 4 and S4]) used in the statistical analyses; such changes in spatial variability on any scale may indicate changes in the distribution of limiting resources (Yang et al., 2009; Fujita et al., 2010; Koide and Peoples, 2012). The use of sensors to quantify a soil attribute or variable, whether directly (e.g., EM_H and EM_V), or indirectly (e.g., N, IC and OC), provided a reliable method to measure the within-plot (e.g., among grids) variance of crop performance; the latter was considered (Ma et al., 1999; Jaradat and Weyers, 2011) a side effect of varying stress conditions under different management practices. Theoretically, however, when all plant-growth requirements are abundantly available, a uniform pattern of plant growth and performance is minimized or even eliminated (Dobermann and Cassman, 2002; van Noordwijk and Cadesch, 2002) unless subjected to temporal variation (Fig. 2).

Empirical modeling of crop performance

Proper statistical analyses procedures are needed to identify the sources and magnitude of spatial variation, especially when modeling the performance of a new crop such as Cuphea (Webster, 1997; Bayer et al., 2012; Warton et al., 2012), because spatial variation is assumed to be random and its impact on crop performance can be masked by temporal variation (Jaradat and Weyers, 2011). The PLS regression approach provided more parsimonious models for predicting oil content and oil yield than ordinary linear regression (Esbensen, 2005; Payne et al., 2007; Bayer et al., 2012); however, with different levels of certainty based on independent variables and factors used in the stepwise PLS regression models (Table 5). Descriptors of the multivariate PLS models represent the percent variation within the data set that can be explained by the model (i.e., R^2); and how accurately the model can be expected to predict new data (i.e., Q^2) (Esbensen 2005). The use of soil nutrient ratios, as surrogate variables of soil series, suggested that their variation accounted for larger and more significant portion of total variation in oil content and oil yield (31 and 36%, respectively). However, these values were slightly smaller than the respective values of 40 and 38% when seed nutrient ratios were used to build the PLS regression models (Table 5). Antagonistic relationships between three nutrient ratios involving, N, P and S in soil (i.e., N:P, N:S, and P:S; Table 5) with opposite loadings on PLS1 as compared to C:N and C:P, suggest that nutrients, and therefore their ratios, undergo different biochemical transformations and associations leading to differences in their effects on oil content and oil yield as was confirmed earlier in Cuphea (Jaradat and Rinke, 2009). In this regard, both P and S displayed similar trends in all soils except Parnell (Fig 7 and 8). Negative and positive loadings of all nutrient ratios in seed on oil content and oil yield, respectively, confirm earlier findings in that the dynamics of C:N and C:P differed from the remaining ratios as the nutrients move from soil and are deposited in seed (Jaradat and Rinke, 2009). Seed oil content may be more associated with the C:N ratios in shoots and roots of oilseed crops rather than with the absolute amount of accumulated C (Fei et al. 2013); a speculation which can be partly supported by the positive and relatively large C:N and IC loadings on PLSC1 predicting oil content for Barnes (Fig. 7A) and Hamerly (Fig. 7C), but not Barnes-Buse and Parnell. We used end-of-season measurements and estimates of independent factors and dependent variables in modeling crop performance. Although the validity and interpretation of modeling crop response to soil properties which may change during the cropping season (e.g., soil nutrients and their ratios) using data collected at the end of the growing season have been questioned (Shattar and McBratney, 1999), we developed sets of precisely-measured covariates (Table 3, 4 and 4S) and quantified functional, rather than statistical relationships between variables (Fig. 6) to overcome this limitation. Additionally, we validated results of the current study on the basis of earlier findings of joint soil and plant (including seed) nutrient sampling and analyses throughout the growing season (Jaradat and Rinke, 2009).

Materials and Methods

Soil series

Four soil series (Soil Survey Staff 2006) were identified in the experimental area selected for the 2-year experiment at the Swan Lake Research Farm, Morris, MN, USA (45°41′11.15" N, 95° 48′ 02.49" W, elevation 370 m). As Mollisols (Veenstra and Burras, 2012), they are generally the soil order widely used for agriculture in the Midwestern USA; and they are characterized by thick, dark, organic matter-rich surface horizons and relatively high base saturation throughout the profile (Soil Survey Staff, 2006); the four soils are:

(1) The Barnes glacial soil series was identified as the major soil type in the experimental site. The Barnes soil series is considered as a clay loam with a plane slope of ~1% on a ground of moraine. It has a calcareous subsoil horizon and typically is neutral to slightly alkaline in the surface 20 cm. This soil series is classified as Fine-loamy, mixed, superactive, frigid Calcic Hapludols,

(2) Barnes-Buse: Gently sloping to hilly and steep, well-drained soils that are loam or clay loam throughout. This series consists of very deep, well drained soils that formed in loamy glacial till on moraines; they have slopes of 3 to 60 percent; mean annual precipitation is about 500 mm; and mean annual air temperature is about 5 °C. They are classified as Fine-loamy, mixed, superactive, frigid Typic Calciudolls,

(3) Hamerly series consists of very deep, somewhat poorly drained soils that formed in calcareous loamy till. Permeability is moderate in the upper horizons and moderate or moderately slow in the lower horizons. These soils are on flats on lake plains and on convex slopes surrounding shallow depressions and on slight rises on till plains. They have slopes ranging from 0.0 to 3.0 percent. Mean annual air temperature is ~ 5 °C, and mean annual precipitation is ~450 mm. The series is classified as Fine-loamy, mixed, superactive, frigid Aeric Calciaquolls, and

(4) Parnell series consists of very deep, very-poorly, and poorly drained soils that were formed in water-sorted sediments from glacial drift in depressions, swales and drainage ways on glacial moraines. These soils have slow permeability. Slopes range from 0.0 to 3.0%. Mean annual precipitation is about 500 mm; and mean annual air temperature of ~ 5 °C. This soil series is classified as Fine, smectitic, frigid Vertic Argiaquolls.

Plant material

A partial seed retention selection (PSR23) from a cross between *Cuphea lanceolata* and *C. viscosissima* (Knapp and Crane 2000) is a potential new oilseed crop; its main fatty acids (i.e., capric, lauric, and myristic) are used in the detergents, lubricants, cosmetics and confectionary industries. *Cuphea lanceolata* is a protandrous, self-compatible, insect-pollinated allogamous diploid with >80% outcrossing rate ($2x = 12$), while *C. viscosissima* is a self-fertile, autogamous diploid ($2x = 12$) and about 30% outcrossing rate. In addition, the two species are inter-fertile, thus allowing for combining desired traits from both in new genotypes.

Field experiment

A field experiment was conducted in 2005 and 2006 cropping seasons on two transects, each covering four soil series (i.e., Barnes, Barnes-Buse, Hamerly and Parnell). These transects were of equal dimensions and each encompassed 36 equal grids measuring 360 x 3 m; each grid was identified by its main soil series. Growing degree days (sowing to harvest, with a base temperature of 10°C) in 2005 and 2006 were 1180 and 1230, respectively; whereas, the respective amounts of total rainfall during the same period were 505 and 253 mm, or 28% above and 36% below the log-term (100 last years) average for the location. Planting was performed using a Wintersteiger® seed drill with six rows (360 m long and 60 cm between rows). Cuphea seed (65% germination rate in laboratory test) was planted at a rate of 12.54 kg ha^{-1} on May 11, 2005 after soybean and 11.2 kg ha^{-1} on May 8, 2006 after wheat. Management practices included (1) fertilizer (84-34-34 kg ha^{-1} N-P-K) broadcast application in both years which was based on earlier (Berti et al., 2007; Jaradat and Rinke, 2009; Jaradat 2012) research results, (2) several pre- and post-emergence herbicide applications in order to guarantee no weed competition with Cuphea as a semi domesticated crop and to verify the efficacy of these herbicides Herbicide applications consisted of ethalfluralin {N-Ethyl-N-(2-methyl-2-propenyl)-2,6-dinitro-4-(trifluoromethyl)benzenamine} which were applied pre-sowing and incorporated at 0.705 kg active ingredient (ai) ha^{-1} and mesotrione {2-[4-(methylsulfonyl)-2-nitrobenzoyl]-1,3-cyclohexanedione} applied post emergence at 0.085 kg ai ha^{-1} with a ground sprayer in 2005; and 5-cyclopropyl-4-(2-methylsulfonyl-4-trifluoromethylbenzoyl) isoxazole applied pre-emergence with ground sprayer at 0.064 kg ai ha^{-1} and sethoxydim {2-[1-(ethoxyimino)butyl]-5-[2-(ethylthio)propyl]-3-hydroxy-2-cyclohexen-1-one} applied post emergence at 0.20 kg ai ha^{-1}, combined with 1.12 kg ha^{-1} hyper-oil with a ground sprayer in 2006. At harvest, the three central rows per plot (1.60 m x 9.0 m) from each grid were combine-harvested on September 15, 2005 and September 6 and 26 in 2006. Seed samples were dried in an air-forced oven at 45°C to a moisture content of 15%, and then used for chemical analyses.

Physical and chemical analyses

Soil sampling and soil analyses. Two soil samples were taken at the start and end of the growing season in 2005 to a depth of 0-15 and 15-30 cm and three soil samples in 2006 to a depth of 0-15, 15-30 and 30-45 cm from each grid within each soil series then used in physical and chemical analyses. Data for each soil variable derived from the chemical analyses of a composite soil sample from each grid was used in the final statistical analyses. Soil moisture content was estimated on soil samples from each grid within each soil series at mid-season (July) and right after harvest (October) in each year using gravimetric method. Soil moisture estimated after harvest was used as a covariate in mixed models after accounting for total rainfall in each year; whereas, nutrient estimates at the end of each season were used in statistical analyses as described in *2.5* below, after accounting for initial estimates at the start of the season. Electrical conductivity was measured after harvest using the EM-38 instrument (Geonics EM-38, Mississauga, Ontario, Canada; www.geonics.com) mounted on a 3-m long cart supported by four spoke-wheeled pneumatic tires in order to avoid interference from metallic objects. For field-scale continuous electrical conductivity measurements, the EM-38 was attached to the rear of a 4-wheel all-terrain vehicle. Electrical conductivity data obtained simultaneously from the EM-38 horizontal (EM_H) and vertical (EM_V) sensors and from a differential Geographic Positioning System (GPS) were integrated and stored for further data processing and statistical analyses, then the weighted apparent electrical conductivity (ECa; expressed in dSm^{-1}) was calculated as

$$ECa = \alpha_V \times EM_V + \alpha_H \times M_H,$$

and was used in subsequent statistical analyses after a temperature correction (~ 1.09 to 1.12) was made according to Huth and Poulton (2007). Values for the weighting coefficients α_V and α_H (0.77 and 0.23, respectively) were chosen to minimize spatial bias in the surface ~1.0 m of the soil profile (Huth and Poulton, 2007). In order to account for differences in soil texture, the electrical conductivity of a saturated soil extract (ECe; dSm^{-1}), as a reliable measure of salinity for comparing between soil series, was performed on sub-samples of each soil sample, then used to calibrate the EM-38 readings. Ammonium- and nitrate-N (NH_4^+-N and NO_3^{-}-N, respectively) were extracted from dried soil with 1 M KCl using a 1:10 soil:solution ratio, concentrations were measured using an Alpkem Auto-analyzer (Pulse Instruments Ltd., Saskatoon, SK) by standard colorimetric Berthelot (NH_4^+) and Griess–Ilosvay (NO_3^-, following Cd reduction to NO_2^-) methods (Mulvaney 1996). Soil pH in H_2O and $CaCl_2$ were measured using a 2:1 water or buffer to soil ratio, then averaged for each soil sample. Determinations of total C and N for both soil and plant materials were made with a LECO CN-2000 instrument (LECO Corp., St. Joseph, MI). Soil inorganic C was determined as described by Wagner et al. (1998). Available P was determined using the Olsen P method (Olsen and Sommers, 1982), and total oil determinations were made using multiple hexane extractions according to Soxhlet method (AOAC 963.15) (AOAC, 1983).

Nutrient analyses

For the purpose of nutrient analyses, soil and seed samples were dried at 45 °C in a forced air oven for one week or until no further reduction in weight occurred. Seed materials were ground in a coffee grinder and placed through a 1-mm screen while soil samples were ground through a 40 mesh stainless steel Wiley mini-mill (Thomas Scientific, Swedesboro, NJ, USA). Nutrients were determined in soil and seed samples from each of 36 grids separately. Digestion of soil and seed samples followed the US-EPA 5051 method; this procedure was adapted using the Mars Xpress Microwave System from CEM (CEM Corporation, Mathews, NC, USA) sample preparation note XprAG-1. This microwave procedure uses 55 ml Teflon tubes in a 40 unit carousel. A 0.5 g sample weight was digested with 6.5 ml nitric acid (70% Trace Metal Analysis, TMA) using a 15 minute ramp program set to a power maximum of 1200 W and held for 15 minutes. The samples were allowed to cool to room temperature and transferred to 50 ml volumetric flasks and taken to volume with Milli-Q water (Millipore Corporation, Billerica, MA, USA). Smaller samples were taken to 25 mL with adjustments made for nitric acid (HNO_3) concentrations. Analysis was completed using the Varian Vista-Pro CCD (Charge Coupled Device, Varian Incorporated, Palo Alto, CA, USA) simultaneous inductively coupled Plasma-optical emission spectroscopy (ICP-OES) instrument (Rayan, 2013). MNUSDA-STD 1-A and MNUSDA-STD 2 (Inorganic Ventures, Lakewood, NJ, USA) were prepared as elemental standards (Masson et al., 2010).

Statistical analyses

Several univariate, bivariate and multivariate statistical procedures were employed in exploring and modeling the relationships and interactions between and within groups of variables in the study. Each variable was subjected to Shapiro-Wilks W test for normality (StatSoft Inc., 2012), and if the W test statistic was significant, data was log- or square root-transformed for statistical analyses, then back-transformed for reporting. The assumptions of multivariate normality were evaluated (Payne et al., 2007) then the outliers, if any, were removed from statistical analyses. Twenty-five variables measured or estimated on each soil series (Table 1) were subjected to analyses of variance among soil series and among grids within each soil series. Statistical relationships between nutrients in soils and seed were estimated using canonical correlation and canonical discriminant analyses; a similar procedure was performed to estimate relationships between nutrient ratios (C:N, C:P, N:P, N:S, and P:S) in soil and seed.

Canonical discriminant analysis (CDA)

Canonical Discriminant Analysis was used to determine if nutrient contents or nutrient ratios, as continuous variables, can discriminate between soil series, as categorical variables, and to estimate the standardized discriminant coefficients for the first canonical discriminant root contributing to the discrimination process. In CDA, more distinct differentiation between categorical (qualitative) variables such as soil series can be achieved as compared with univariate analysis. The CDA can separate the effects of "among-soil series category" from those of "within-soil series category" thus maximizing the overall discrimination power (StatSoft Inc., 2012; Payne et al., 2007). In addition, variance explained by the first canonical root, and percent correct classification of each soil series were estimated.

Reduced main axes models (RMA; Type II Regression)

RMA models were used to determine the scaling exponents of macro- and micronutrients in seed versus their contents in each of the four soil series since functional relationships were sought between these interdependent nutrients, which are also subject to measurement error (Niklas, 2006). Prior to RMA analyses, nutrient contents and ratios were log-transformed, in which case their relationship approximately followed a power law, $Y = aX^b$. The scaling exponent '*b*' is the slope on log-transformed axis, and the magnitude of this parameter describes how steep the relationship between *Y* and *X* is. The 'proportionality' coefficient '*a'*, which is related to the elevation on the log-log axes, is used to explore how *Y* values of a given *X* will be (Warton et al., 2012). A *t*-test in conjunction with the standard error for *b*RMA was used to determine whether the slopes differed significantly from one |1.0| (i.e., isometry), and the coefficients of determination (R^2) were used as measures of the proportion of the total variation in *Y* explained by its linear relationship with *X* .

Mixed models

Mixed models, including fixed and random factors, were employed to estimate the level of significance of fixed factors and the amount and level of significance of variance accounted for by random factors on Cuphea's performance (i.e., seed weight, g; seed yield, kg ha^{-1}; seed oil content, %; and oil yield, L ha^{-1}) and on five nutrient ratios in the seed (i.e., C:N, C:P, N:P, N:S, and P:S). Soil chemical attributes (soil water content, ECe, ECa, NO_3, NH_4, and pH), and nutrient ratios in soils (i.e., C:N, C:P, N:P, N:S, and P:S) were used as covariates in the statistical analyses as appropriate. The level of significance of fixed factors was expressed as *p(F)*, and the variance accounted for by random factors was expressed by *p(z)* (Payne et al., 2007).

Partial least squares (PLS) regression

PLS regression is a bilinear modeling approach where information in the independent variables is projected onto a small number of latent variables (PLS components) and the dependent variables are actively used during the estimation process of latent PLS components (Esbensen, 2005). Calibration and validation PLS regression models were developed for oil content and seed yield in each soil series using all variables measured on soils and seed. Stepwise PLS validation models were developed for oil content and seed yield using years, soil series and nutrient ratios in soils and seed as independent variables; the reliability of the first component in each of these models was tested using cross-validation, and by contrasting prediction (R^2) and validation (Q^2) coefficients of determination of each model. Statistical tests were performed using relevant modules in STAISTICA v. 10 (StatSoft Inc., 2012) for univariate, bivariate and multivariate analyses. GenStat v.10 (Payne et al., 2007) was used to perform mixed models and variance components analyses. The Standardized Major Axis Tests and Routines (SMATR 3), an R package for estimation and inference about allometric lines Warton et al., 2012), was used to perform reduced major axes analyses, and The Unscrambler v.10.1 (CAMO, 2011) for building and testing calibration and validation PLS regression models.

Conclusions

The current scientific knowledge of Cuphea's response to nutrients and environmental conditions is not sufficiently robust to make significant improvements in its nutrient use efficiency. Reliable strategies for site-specific nutrient management of Cuphea, as a potential oilseed crop, can be based on understanding of quantitative multivariate relationships between seed yield, oil content and oil yield, in one hand, and on nutrient dynamics and functional relationships in soil and in seed, on the other. In addition, proper temporal linkages between nutrient supply and crop demand need to be taken into consideration. Classical univariate statistical analyses procedures cannot separate the different sources of spatial and temporal variation affecting nutrient contents and other soil attributes. The use of multivariate analyses procedures to understand multivariate structures, helped to overcome some of the limitation imposed by multicolinearity, and non-random or regionalized variation of soil attributes and nutrients. Nevertheless, only a fraction of the observed variation in oil content and oil yield could be explained by any one of the measured factors, indicating that a number of soil properties contributed to this variation. We developed response functions of Cuphea to spatial variation based on empirical modeling of the impact of four Mollisols on the performance of the crop as quantified by seed yield, oil content and oil yield. Although most of the measured soil properties varied spatially, only a few were responsible for variation in crop performance. The spatial cause-effect relationships we developed between nutrient levels and each of oil content and oil yield can be predicted; and potentially generalized, and extrapolated to new oilseed crops.

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