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INVITED ARTICLE

Simulated climate change deferentially impacts phenotypic plasticity and stoichiometric homeostasis in major food crops

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ABSTRACT

Grain yield and product quality responses of major food crops to variation in resource availability continue to be important considerations in agronomic research, particularly under abiotic stresses. Indices of grain quality and phenotypic plasticity of crop cultivars with C_3 or C_4 metabolic pathways and producing seed with either carbohydrate, protein, oil; or a combination of carbohydrate-protein or oil-protein as their major product, were quantified for six years under two phases of single and multiple abiotic stresses. Decreasing resource availability caused by short growing season and high population density, singly or in combination, resulted in significant changes in allometric relationships among most traits under study. Temporal quantitative and qualitative differences between "heatmaps" of stress phases, partitioning and analysis of total variance due to fixed and random factors, and functional relationship at hierarchical levels of organization, indicated a shift over time of phenotypic plasticity and quality indices. Moreover, relationships of phenotypic plasticity and quality index with biomass, grain yield, macro- and micronutrients, and nutrient ratios were largely modulated by differences between crop products within metabolic pathways. However, further research is needed for in-depth understanding and insights into the interdependencies of the large number of traits that crop plants should optimize to produce economic yield combined with adequate nutritional quality under abiotic stress.

Keywords: Abiotic stress; Allometry; Ecophysiology; Metabolic pathway; Nutrients; Phenotypic plasticity; Quality index

INTRODUCTION

Grain yield, as the 'agricultural fitness' indicator of interest to agronomists and producers is increasingly subjected to abiotic stresses, and all crop plants express some degree of phenotypic plasticity when subjected to abiotic stress (Sadras et al. 2016; Quintero et al. 2018). Agronomists and breeders of field crops considered plasticity, which is trait- and environment-specific, as an undesirable phenomenon; however, perspectives on that, being borrowed from ecological studies of wild plant populations (Müller et al. 2000) are changing (Nicotra et al. 2010; Tokatlidis 2017; Richardson et al. 2017). Maintaining an acceptable nutritional grain quality under abiotic stress is critical for human nutrition, end-use functional properties, as well as commodity value (Nuttall et al. 2017; Daryanto et al. 2017). In this context, grain quality, which is influenced by genetics, management and the environment, was defined as an integrated measure of physical (seed weight and dimensions) and compositional (protein, oil, carbohydrates and nutrient contents) properties. Abiotic stress continues to pose a significant challenge for delivering grain of consistent quality in the future due to the complex interactions of climatic, environmental and edaphic factors and their interactions on grain yield and its quality (Sadras and Richards 2014; Shim et al. 2017). Larger biomass and grain yield are expected under favorable conditions if crop plants can maintain stoichiometry between nutrients; and if plant growth is not constrained by nutrient supply from the soil environment (Pilbeam 2015). Several plasticity indices are available in the literature to quantitatively estimate phenotypic plasticity (Richardson et al. 2017; Valladares et al. 2007); however, they rendered dissimilar results, with crossovers in crop species or cultivar phenotypic plasticity rankings. Therefore, standardized phenotypic plasticity estimate based on variance ratio between the stressed and the control treatments have been advocated as a measure of phenotypic plasticity (Sadras et al. 2016).

Nutrient composition of field crop seed represents a developmental end-point that summarizes the life history

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of a crop plant. It reflects the presence of a dynamic system and a network of macro- and micro-nutrients that are controlled by several interacting factors (Baxter 2015). In addition, genotypes within a crop species may respond in growth, biomass allocation and nutrient accumulation differently to abiotic stresses (Wang et al. 2017). The ability of plants to allocate biomass, and therefore nutrients, to structural, metabolic and reproductive organs (i.e., roots and stems, leaves, and seed, respectively) depends on many biotic, abiotic, and management factors and their interactions (Rose et al. 2015; Halford et al. 2014). Biomass partitioning is considered a strong driver of the capacity of crop plants to take up carbon, water and nutrients for future use. However, allocations to different plant organs is mediated by phenotypic plasticity; which is a means of modifying plant growth and development in response to the environment (e.g., abiotic stresses) (Müller et al. 2000; Poorter et al. 2012). Allometric allocation and relationships have been reported in crop plants because of, for example, water and nutrient deficiencies (Huang et al. 2010) and population densities (Ciampitti et al. 2013; Ciampitti and Vyn 2013).

Although crop plants exhibit wide variation in nutrient contents and nutrient ratios, they exhibit higher degree of 'stoichiometric homeostasis' than previously known. Therefore, nutrient stoichiometry is expected to reflect the effects of adjustment to local growth conditions, among other factors (Elser 2010). Plant stoichiometry displays size scaling, as nutrient content decreases with increasing plant size (i.e., the dilution effect) and in response to environmental factors (Poorter et al. 2012; Liu et al. 2016). There is a growing body of empirical evidence on how plant biomass, grain yield and nutrients, and subsequently the nutritional quality of end-products, respond to and are impacted by abiotic stressors (Baxter 2015; Liu et al. 2016). Abiotic stress can induce considerable changes in the biochemical and chemical composition and quality of crop seeds (Halford et al. 2014). Crop plants with the C_3 and C_4 metabolic pathways differ in their nutrient status and are expected to respond differently to a changing climatic factor (Adjorlolo et al. 2015). However, very few cases considered the analysis of variability in nutrient allocation to seeds in relation to allometric patterns; or to deviations from the allometric trajectory (Weiner 2004; Niklas and Hammond 2014). Several biometrical procedures have been developed to assess the impact of abiotic stresses on nutrient dynamics in crop plants (Reich et al. 2010; Xu 2016). The larger the number of nutrients included in the analyses, the more powerful the biometrical test, especially when multivariate statistical procedures are employed (Wang et al. 2017; Ciampitti et al. 2013). The objective of this study was to quantify inter- and intra-specific variation in crop phenotypic plasticity under abiotic stress and model its impact on a standardized nutritional quality index in crop species producing carbohydrates, protein, oil, carbs-protein, or oil-protein as their end-product under single and multiple abiotic stressors.

MATERIALS AND METHODS

Design and function of the field experiment

Multiple stresses were imposed on five crops in a split-split-plot (in space and time) field experiment in two phases by controlling the length of the growing season (in Growing Degree Days, GDD) and population density (Table 1) under otherwise typical management practices for each crop in the upper Midwest, USA. Additional edaphic stress was imposed in the field during Phase I by planting the same genotype on the same experimental plot for three consecutive years; then released during Phase II. Abiotic stresses (LN=late planting and normal population density; NH=normal planting date and high population density; and LH=late planting date and high population density) were contrasted with the control (NN=normal planting date and normal population density) for two cultivars in each of five crop species. For each cultivar and species, plants were sampled at the late vegetative (stems and leaves), physiological maturity (stems, leaves and immature seed), and full maturity stages (stems, leaves and mature seed).

Samples were used to estimate plant and organ dry weight, then used for chemical analysis. This part of the study reports on data collected mainly on seeds, as the final product of each cultivar and crop species.

The design and physical layout of the field experiment was approriate to monitor the development and collect relevant data on all crops under study (Table 1). The planted area per crop and replicate was large enough to sample plants during the late vegettaive, physiological maturity and full maturity stages with compromizing the final area for harvest in order to estimate biomass and grain yield of each crop. The number of samples taken for over the 6-year period ranged from 631 for soybean to 862 for corn, an average of between 100 and 140 samples per year and crop. Data were collected on plot, sub-plot (i.e., sampling), single plant, and random seed samples. This part of the study reports on measured (biomass, grain yield, and nutrient concentrations in seed harvested at the physiological and full maturity growth stages) and estimated (phenotypic plasticity, quality index, and nutrient ratios) variables under two successive abiotic stress stages, each with three-year duration; the second phase differes from the first by including a crop rotation factor in order to remove part of the edaphic stress which was imposed on all crops during the first phase.

Table 1: Design of the split-plot (in time and space) experiment in a randomized complete block layout, including stress treatments, factors and experimental units

Experimental design	Split-plot in randomized complete block design				
Main plots	**Crops**				
	Corn	**Chickpea**	**Safflower**	**Wheat**	**Soybean**
	Z. mays	***C. arietinum***	***C. tinctorius***	***T. aestivum; T. durum***	***Glycin max***
Metabolic pathway	C_4	C_3	C_3	C_3	C_3
Major product	Carbs	Protein	Oil	Carbs-protein	Oil-protein
No. of genotypes	2	2	2	2	2
No. of replicates	4	4	4	4	4
No. of samples	862	653	804	400 bread & 400 durum wheat	631
Sub-plot dimensions, m	12×6	12×6	12×6	12×6	12×6
Plants/ha (million)	0.085	0.063	0.045	1.45	0.065
Sowing date (Julian)	125±5	120±10	120±10	110±5	125±5
N-P-K application	Pre-planting, based on soil test				
Sub-plots	Stress treatments per crop				

Stress phase	**Population density**	**Length of the growing season (GDD)**	
I		Normal planting date	25% (GDD) shorter than normal
	Normal (by crop)	Control (NN)	Single stress (NS) (short GDD)
	25% higher than normal	Single stress (HN) (population density)	Double abiotic stress (HS)
	Crop rotation	No rotation (3 years)	No rotation (3 years)
II			
	Normal (by crop)	Control (NN)	Single stress (NS) (short GDD)
	25% higher than normal	Single stress (HN) (population density)	Double abiotic stress (HS)
	Crop rotation	Crop rotation (3 years)	Crop rotation (3 years)

	Year					
Hundred-year (mean±s.d.)	2006	2007	2008	2009	2010	2011
Rainfall, mm (589±87)	460	550	490	450	570	550
Growing degree days (1930±190) °C	1950	1940	1850	1895	1920	1900
Temperature (14.7±2.8) °C	17.9±4.6	18.2±4.2	16.1±3.9	174.2±4.2	17.8±4.2	17.4±4.7
Photothermal quotient (1.84±0.5) MJ $m^{-2}d^{-1}C^{-1}$>0.0 °C	1.47±0.7	1.95±0.8	1.85±0.5	1.75±0.6	1.68±0.5	1.69±0.7

Abiotic stress treatment combinations (i.e., NS, HN, and HS) provided contrasting abiotic single and double stress levels. In contrast to the control (i.e., normal planting date and normal population density for each crop; NN), each of NS and HN imposed single abiotic stress of 25% shorter length of the growing season and 25% larger population density, respectively; whereas, HS imposed both levels of abiotic stress on crop plants. Planting each crop on the same land area for the first three years (Phase I) subjected crops to an additional edaphic stress, which was removed during Phase II.

Chemical analyses

Samples were dried at 45°C in a forced air oven until no further reduction in weight occurred. Kernels were ground and placed through a 1 mm screen (Thomas Scientific, NJ). Then one subsample was used to determine carbon and nitrogen and another to determine micro-and macro-nutrients. Carbon and nitrogen were determined on samples as percent of dry weight using LECO FP-428 analyzer (LECO, St. Joseph, MI), then the C: N ratio was calculated for each subsample. Percent nitrogen values were used to estimate protein content as N% x 6.25. Determination of micro- (Cu, Fe, Mn, and Zn) and macro-nutrients (Ca, K, Mg, P, and S) followed the procedure outlined in the US-EPA 5051 method (Masson et al. 2010). Details of the procedure are available elsewhere (Baxter 2015).

Statistical analyses

Primary and secondary statistics were calculated for each variable in the study. Several modules in JMP Pro., v. 13.2.0 (SAS Institute Inc. 2016) statistical software packages were employed in performing data management and multivariate statistical analyses. A quality index was estimated for each factor included in the experiment and was based on the normalized nutrient contents (Halford et al. 2014; Liu et al. 2016). The effects of fixed factors and the proportion of total variance accounted for by random factors (Table 1) were estimated; then the best covariance model was estimated for each nutrient and its significance was tested and expressed as R^2 value (Payne 2014).

Multi-way clustering and associations between crop products (x-axis) and agronomic and nutrient traits measured or estimated on seed samples of C_3 and C_4 field-grown crops for three years was performed under each abiotic stress phase. Analyses of variance and variance components analysis were performed using mixed models (i.e., fixed and random factors). Two nutrient ratios (i.e., C: N and C: P) were used as covariates in the variance components analyses due to their effects on other variables (Payne 2014). Boxplots (with median, and 0.25 to 0.75 intervals for each product) were developed for each of phenotypic plasticity at physiological and full maturity stages, and for the quality index at the late vegetative, physiological and full maturity stages. Statistical moments (mean of response, RMSE, and adjusted R^2) and coefficients of quadratic regression equations (β1 and β2) of plasticity on grain yield were calculated for each crop product at each abiotic stress phase.

Finally, statistical moments, coefficients of reduced maximum axis (RMA) regression (i.e. scaling exponent or slope, α_{RMA}; and scaling factor or intercept, β_{RMA}) were calculated for the standardized quality index as a function of standardized phenotypic plasticity at different levels of organization within each abiotic stress phase. Allometric relationships (Poorter et al. 2012) were estimated using reduced major axis (RMA). Prior to RMA analyses, variables were log-transformed, in which case their relationship approximately followed a power law. In this model (Type II Model), the allometric relationship between any two variables X and Y can be described by the equation: $Y = bX^a$ where "*a*" is the scaling exponent, or slope, and "*b*" is the allometric coefficient or "scaling factor", or the Y intercept (Xu 2016). This regression procedure is recommended when the variables of interest are biologically interdependent and subject to unknown measurement errors (Niklas and Hammond 2014). Factor effects on estimates of the scaling exponent (α_{RMA}) (mean ± SE) in allometric regression models and test statistics (Jack-knifed R^2 and *p*-value) were estimated for the functional relationship of a quality index. A t-test in conjunction with the standard error for α_{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.

RESULTS

Multi-trait clustering and association

Multi-way clustering and associations between crop products (x-axis) and agronomic and nutrient traits measured or estimated on seed samples of C_3 and C_4 field-grown crops for three years under abiotic stress phase I are presented in Fig. 1 (see Table 1 for details). Two classification factors (end products and PS or metabolic pathway) separated the whole data set derived from stress phase I into five main clusters; four of which were within C_3 and one within C_4 metabolic pathways on the basis of measured and estimated variable (y-axis). The distance scale (y-axis) indicated the proximity of carbohydrates and carbohydrates-protein products in one sub-cluster (~0.50 clustering distance), oil-protein formed an intermediate cluster (~0.75 clustering distance) beetween the first and

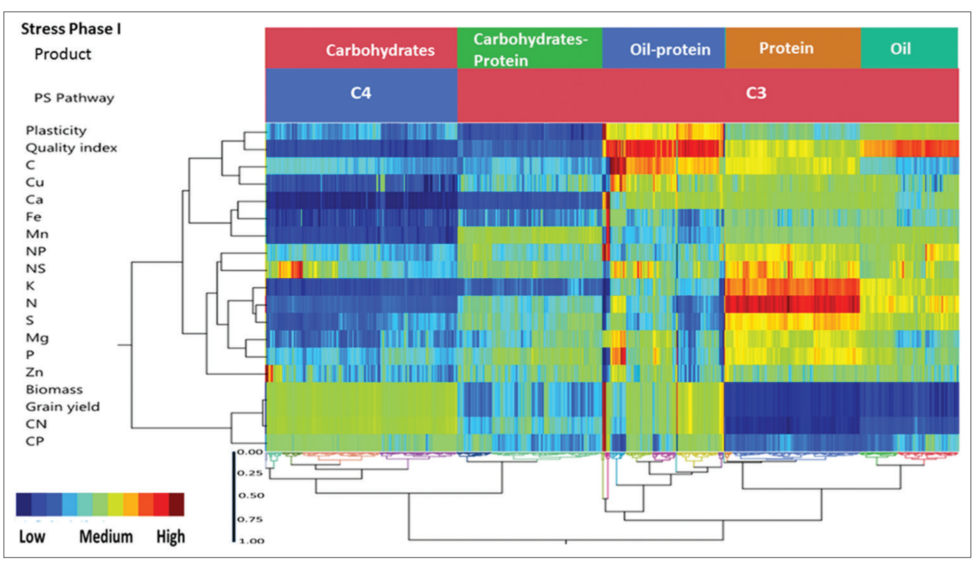


Fig 1. Multi-way clustering and associations between crop products (x-axis) and agronomic and nutrient traits measured or estimated on seed samples of C_3 and C_4 field-grown crops for three years under abiotic stress phase I (see Table 1 for details).

last two clusteres which were formed of protein and oil products. However, a large number of sub-sub-clusters with specific trait combinations have been identified (data is available upon request). Combinations of quantitative low-medium-high trait levels can be visually identified; whereby, "hot spots" of desirable large or small levels of one or maore traits are referenced by product-metabolic pathway and trait associations (i.e., heatmap).

Four main clusters of measured and estimated variables (y-axis) separated biomass, grain yield, C:N and C:P from the remaining variables at the largest distance. Most macronutrients, in addition to N:P and N:S constituted the second cluster; micronutrients (except Zn, which was clustered with P and other divalent cations) formed a third cluster; while, plasticity, quality index and C formed the last cluster. Comparatively, the protein, oil-protein, and oil products, in decreasing order, displayed "hot spots" for combinations of plasticity-quality indices; and combinations of several macronutrients, in addition to high-to-moderate values of N:P and N:S ratios. The heatmap also showed blocks of low values of biomass and associated traits in protein and oil-protein products, as well as moderate values for the same variables in C_4-carbohydrates product. The dominating effects of C over N and P were demonstrated in C:N and C:P ratios being clustered with biomass and grain yield, while the N dominated ratios (N:P and N:S) were clustered with the divalent cations. In addition to the large-scale clusters, there were small clusters forming specific trait combinations, such as P, Mg and Zn; and Fe and Mn; as well as clusteres with moderate K across protein, oil, and oil-protein products, in decreasing order; and another with moderate-to-high N:P and N:S ratios across most products.

Multi-way clustering and associations between crop products (x-axis) and agronomic and nutrient traits measured or estimated on seed samples of C_3 and C_4 field-grown crops for three years under abiotic stress phase II are presented in Fig. 2 (see Table 1 for details). Some of the salient features of clusters, sub-clusters and trait associations with certain products or metabolic pathways in Phase II differed from those in Phase I. Three main clusters can be intified; these were carbohydrates, which was at the largest distance (1.0 clustering scale) from the second (protein and oil-protein), (~0.60 clustering distance) then the third (carbohydrates-protein and oil; clustered at ~0.50 distance) cluster. Each one of the three clusters was composed of several sub-clusters at increasing levels of associations, thus forming a largely different patterns of "hot spots" during Phase II.

Although plasticity and quality index, on one hand, and biomass, grain yield, C:N and C:P on the other, remained largely unchanged; most other variables (y-axis) formed a hierarchy of different clusters. All micronutrients, along with Ca and Mg, clustered around P; while, the remaining bivalent cations clustered with N:P and N:S. A larger number of "hot spots" can be identified in Fig. 2; the largest in magnitude are those associated with quality index (oil-protein, protein and oil, in decreasing order), as well as those associated with protein and the macronutrients K, N, S and N:P and N:S ratios. Micronutrients were involved in forming sporadic (e.g., Cu in oil-protein; Fe in protein and oil-protein) or extensive (e.g., Cu and Zn in oil-protein); while N:P and N:S were involved in large scale clusters in the protein product.

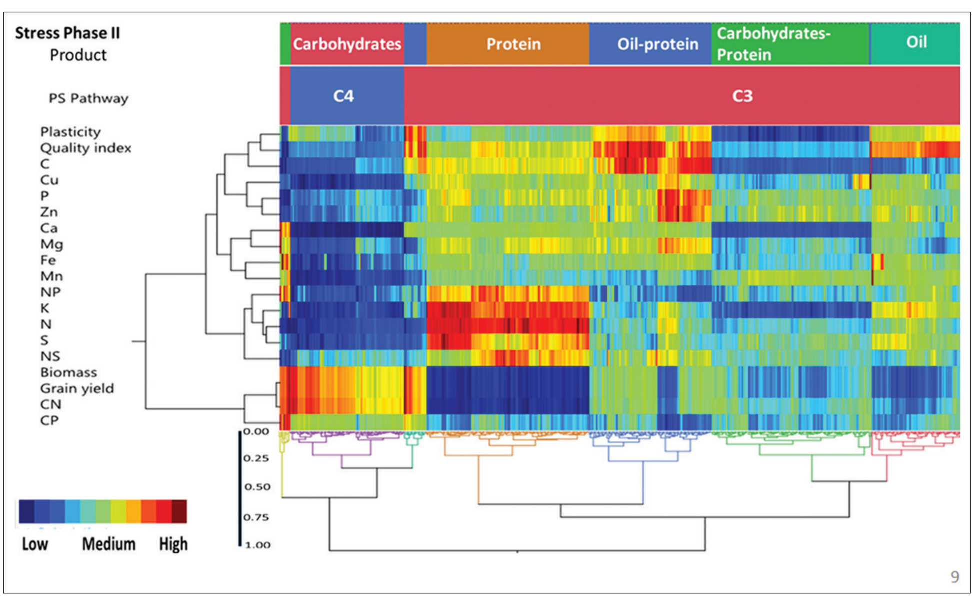


Fig 2. Multi-way clustering and associations between crop products (x-axis) and agronomic and nutrient traits measured or estimated on seed samples of C_3 and C_4 field-grown crops for three years under abiotic stress phase II (see Table 1 for details).

Sources of trait variation

Analyses of variance and separation between product means of grain yield, quality index, plasticity and ratios between nitrogen and each of phosphorus and sulfur in response to two phases of abiotic stress are presented in Table 2. Variation in three agronomic traits (grain yield, plasticity and quality index) and two nutrient ratios (N:P and N:S) in crops producing one or more of carbs, protein and oil, indicated extensive and significant differences within and among stress phases. Standardized grain yield estimates in Phase I were significantly largeer for carbs, carbs-protein and oil-protein producing crops than those producing only protein or oil; however, differences between stress phases were significant for oil (1.44 vs. 1.87) and oil-protein (2.21 vs. 1.86) producing crops. Although there were significant differences between estimates of quality index within each stress phase, none were found among stress phases. Phenotypic plasticity estimates ranged from 0.59 (oil) to 0.84 (oil-protein) in stress phase I, and from 0.65 (carbs-protein) to 0.81(oil-protein) in stress phas II. Significant differences were found between crop products within each stress phase; as well as significant differences in carbs (0.64 vs. 0.72) and oil (0.59 vs. 0.73) phenotypic plasticity estimates between stress phases. Fewer significant differences between crop products were found for N:P and N:S within each stress phase; however, significant differences between stress phases have been found in 60% of the N:P and N:S estimates between stress phases.

Variance components analyses and effects of fixed factors and covariates (i.e. C: N and C: P ratios) on variables measured or estimated on crop plants under abiotic stress are presented in Table 3. Crop products, as fixed factors, and covariates (C:N and C:P), significantly (p<0.05) affected all five variables. The remaining factors (stress phase and management) and their interactions had inconstant effects on most variables. Significant differences in quality index were observed between stress phases; N:P estimates differed among management practices and their interaction with stress phases; N:S estimates were significantly affected by both factors and their 2-way interactions; while, stress phases and product x management interaction effects on N: P were marginally significant (p=0.07).

Phenotypic plasticity estimates differed significantly among stress phases and among products; however, they were resilient under management and under the interaction of management with stress phases and with crop products.

Random factors (i.e., nested factors and interactions; Table 4), explained significant (p<0.05) portions of total variation (range from 4.2 to 35.1%) in most variables; N:P was the only resilient variable and was not affected by most random factors; however, a sizable portion of N:P variation (31.0%) was explained by different responses of crop products to annual variation within stress phases. This random factor accounted for a minimum of 29.0% of total variation in grain yield to a maximum of 35.1% of total variation in quality index. Otherwise, both N:P and N:S estimates were relatively stable in response to the remaining random factors.

Table 2: Analyses of variance and separation between product standardized means of grain yield, quality index, plasticity and ratios between nitrogen and each of phosphorus and sulfur in response to two phases of abiotic stress; means followed by the same letter within each stress phase (I and II) do not differ significantly (p = 0.05); means in *bold and italics* are significantly (p<0.05) larger than the respective mean of the stress phase

Variables	Least squares means stress phase									
Crop product	Grain Yield		Plasticity		Quality index		N:P		N:S	
	I	II	I	II	I	II	I	II	I	II
Carbohydrates	2.07a	2.49a	0.64c	***0.72***b	0.35d	0.35c	10.46d	10.4b	***21.4***a	18.9a
Protein	1.31b	1.39c	0.76b	0.73b	0.62a	0.58a	***12.35***b	8.6c	16.4b	15.9b
Oil	1.44b	***1.87***b	0.59d	***0.73***b	0.44c	0.49b	13.29a	14.1a	17.4b	***12.2***c
Carbs-protein	2.09a	2.03a	0.68c	0.65c	0.39cd	0.38c	***11.42***cd	10.3b	15.5b	14.0c
Oil-protein	***2.21***a	1.86b	0.84a	0.81a	0.53b	0.57a	***12.74***b	10.5b	***20.7***a	15.8b

Table 3: Variance components analyses and effects of fixed factors and covariates (i.e., C:N and C:P ratios) on variables measured or estimated on crop plants under abiotic stress

Fixed factors	Probability of a larger F						
Variables	Covariates		Stress phase	Product	Management	Stress phase × management	Product × management
	C:N	C:P					
GY	0.001	0.001	0.78	0.0001	0.71	0.15	0.76
QI	0.001	0.001	0.04	0.0001	0.90	0.13	0.91
Plasticity	0.001	0.001	0.03	0.0001	0.93	0.17	0.89
N:P	0.001	0.001	0.07	0.0001	0.15	0.57	0.07
N:S	0.001	0.001	0.19	0.0001	0.04	0.03	0.001

Comparative assessment of phenotypic plasticity

Means (± S.D.) of phenotypic plasticity averaged for each of two abiotic stress phases, physiological and full maturity growth stages of crops producing one or a combination of carbohydrates, protein, and oil are presented in Fig. 3. Phenotypic plasticity estimates were expressed as the variance ratio between treatment combinations within stress phases (NS, HN and HS) and the control (NN) for each of the five crop products at physiological and full maturity growth stages. Phenotypic plasticity estimates under stress phase I and II mirrored each other, although differed among and within maturity stages. There were significant reductions between stress phases in phenotypic plasticity estimates for carbohydrates, protein and oil-protein at physiological maturity; and in plasticity of oil-protein at full maturity. Mean phenotypic plasticity estimate for stress phase I was larger and slightly more variable (0.724±0.08) than its estimate in phase II (0.715±0.04). However, within the physiological maturity growth stage, the respective means differed significantly (0.743±0.09 and 0.680±0.05) and the former was more variable than the latter. At full maturity growth stage, mean phenotypic plasticity estimate during stress phase II was significantly larger (0.722±0.04) than its estimate during stress phase I (0.704±0.05).

Mean comparisons between plasticity estimates for crop products within combinations of stress phase-maturity growth stage indicated the presence of dynamic response patterns in these estimates. At physiological maturity, the ranking of mean estimates for phase I (oil-protein>protein>oil>carbs=carbs-protein) slightly differed from their ranking at phase II (oil-protein=protein>oil>carbs=carbs-protein). However, at full maturity, ranking at stress phase I (oil-protein>protein>oil>carbs>carbs-protein) and at stress phase II (oil-protein>protein>carbs=oil>carbs-protein) indicated some differences in these estimates between and within growth stages. Finally, the [0.25-0.75] range around median values in the boxplots suggested that oil-protein, carbs, and protein, in decreasing order, exhibited large variation in phenotypic plasticity estimates as compared to oil and carbs-protein products.

Table 4: Significant variance components (z < 0.05) and effects of random factors on several variables measured or estimated on crop plants producing one or more of carbohydrates, proteins, and oil under abiotic stress.

Random factors	Percent significant variance (z<0.05)			
Variables	Years (Stress phases)	Years x product (Stress phases)	Years x management (Stress phases)	Years x product x Management (Stress phases)
Grain yield	7.2	29.0	5.3	4.2
Quality index	10.3	35.1	7.3	5.5
Plasticity	12.0	34.9	8.0	10.8
N:P		31.0		
N:S		31.5	5.8	7.2

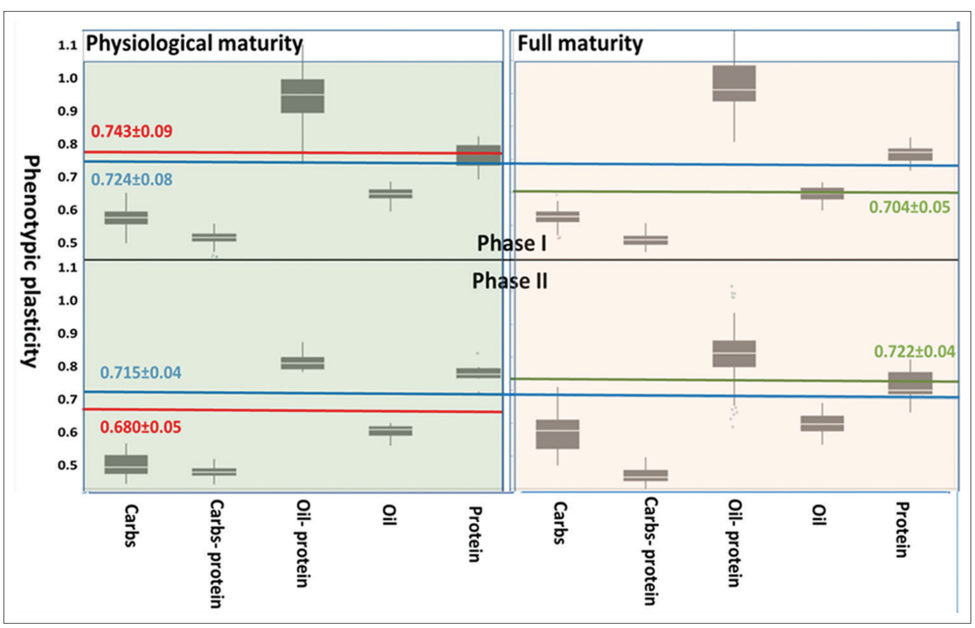


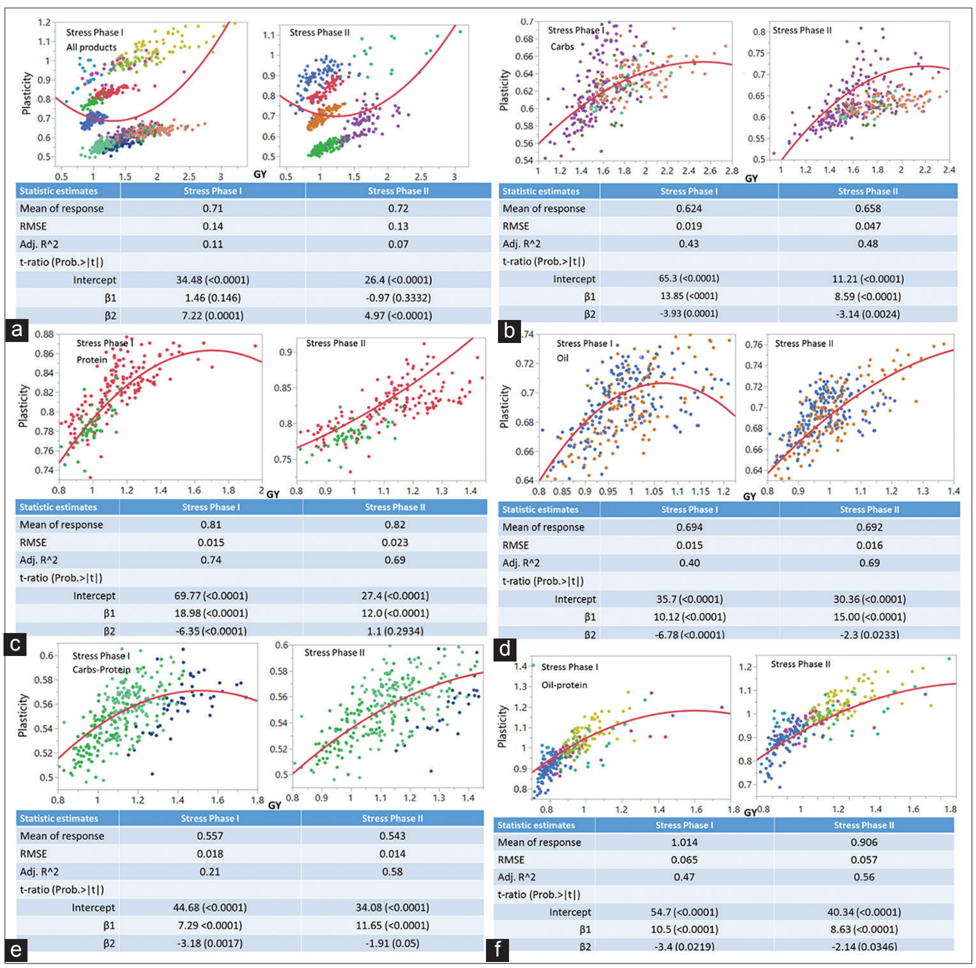
Fig 3. Means (±SD) of phenotypic plasticity averaged for each of two abiotic stress phases, physiological and full maturity stages of crops producing one or a combination of carbohydrates, protein, and oil.

Grain yield-phenotypic plasticity relationships

Statistical moments and coefficients of quadratic regression equations of phenotypic plasticity on standardized grain yield for crops producing carbs, protein, oil, carb-protein or oil-protein under two phases of abiotic stress are presented in Fig. 4. Avergaed over all products, linear regression coefficients (β1) in phase I and II (1.46 and -0.97, respectively) were not significant; however, values of the respective quadratic coefficients (β2 = 7.22 and 4.97) were highly significant. The only non-significant regression coefficient was β2 in protein (1.1), while β1s of individual products were positive, β2s were negative, and both were significant. Plasticity as a function of standardized grain yield averaged over all products in stress phase I (0.71) and II (0.72) and their respective RMSE estimates (0.14 and 0.13) were statistically comparable. However, due to the wide range of variability among plasticity estimates of crop products, the R^2 estimates were extremely low (0.11 and 0.07, respectively). There were some numerical, but not significant, differences in mean plasticity response between stress phases for individual crop products; however, when averaged over stress phases, plasticity estimates displayed significant differences between products, with their R^2 values for stress phase I and II, respectively, as follows: oil-protein [0.47 and 0.56]>protein [0.74 and 0.69]>oil [0.40 and 0.69] >carbs [0.43 and 0.48] >carbs-protein [0.21 and 0.58].

Assessment and prediction of the quality index

Means (±SD) of quality index averaged for each of two abiotic stress phases, three growth stages of crops producing carbs, protein, oil, carb-protein or oil-protein are presented in Fig. 5. Estimated quality index values, whether averaged over stress phase I (0.46±0.08) or II (0.43±0.07); late vegetative growth stage within stress phases (0.41±0.09 and 0.38±0.06); physiological maturity growth stage within stress phases (0.45±0.07 and 0.40±0.04); or at full maturity growth stage within stress phases (0.43±0.07 and 0.46± 0.07), did not differ significantly from each other; however, there were increasing trends in quality index estimates during stress pahese I and II as crops progressed from vegetative (0.41and 0.38, respectively) to physiological (0.45 and 0.40, respectively) then to full maturity (0.53 and 0.46, rspectively) stages. Additionally, there were significant



(a)

Statistic estimates	Stress Phase I	Stress Phase II
Mean of response	0.71	0.72
RMSE	0.14	0.13
Adj. R^2	0.11	0.07
t-ratio (Prob.>|t|)		
Intercept	34.48 (<0.0001)	26.4 (<0.0001)
β1	1.46 (0.146)	-0.97 (0.3332)
β2	7.22 (0.0001)	4.97 (<0.0001)

(b)

Statistic estimates	Stress Phase I	Stress Phase II
Mean of response	0.624	0.658
RMSE	0.019	0.047
Adj. R^2	0.43	0.48
t-ratio (Prob.>|t|)		
Intercept	65.3 (<0.0001)	11.21 (<0.0001)
β1	13.85 (<0001)	8.59 (<0.0001)
β2	-3.93 (0.0001)	-3.14 (0.0024)

(c)

Statistic estimates	Stress Phase I	Stress Phase II
Mean of response	0.81	0.82
RMSE	0.015	0.023
Adj. R^2	0.74	0.69
t-ratio (Prob.>|t|)		
Intercept	69.77 (<0.0001)	27.4 (<0.0001)
β1	18.98 (<0.0001)	12.0 (<0.0001)
β2	-6.35 (<0.0001)	1.1 (0.2934)

(d)

Statistic estimates	Stress Phase I	Stress Phase II
Mean of response	0.694	0.692
RMSE	0.015	0.016
Adj. R^2	0.40	0.69
t-ratio (Prob.>|t|)		
Intercept	35.7 (<0.0001)	30.36 (<0.0001)
β1	10.12 (<0.0001)	15.00 (<0.0001)
β2	-6.78 (<0.0001)	-2.3 (0.0233)

(e)

Statistic estimates	Stress Phase I	Stress Phase II
Mean of response	0.557	0.543
RMSE	0.018	0.014
Adj. R^2	0.21	0.58
t-ratio (Prob.>|t|)		
Intercept	44.68 (<0.0001)	34.08 (<0.0001)
β1	7.29 <0.0001)	11.65 (<0.0001)
β2	-3.18 (0.0017)	-1.91 (0.05)

(f)

Statistic estimates	Stress Phase I	Stress Phase II
Mean of response	1.014	0.906
RMSE	0.065	0.057
Adj. R^2	0.47	0.56
t-ratio (Prob.>|t|)		
Intercept	54.7 (<0.0001)	40.34 (<0.0001)
β1	10.5 (<0.0001)	8.63 (<0.0001)
β2	-3.4 (0.0219)	-2.14 (0.0346)

Fig 4. Statistical moments and coefficients of quadratic regression equations of plasticity on grain yield for crops producing all products (a) carbs (b), protein (c), oil (d), carbs-protein (e) or oil-protein (f) under two phases of abiotic stress.

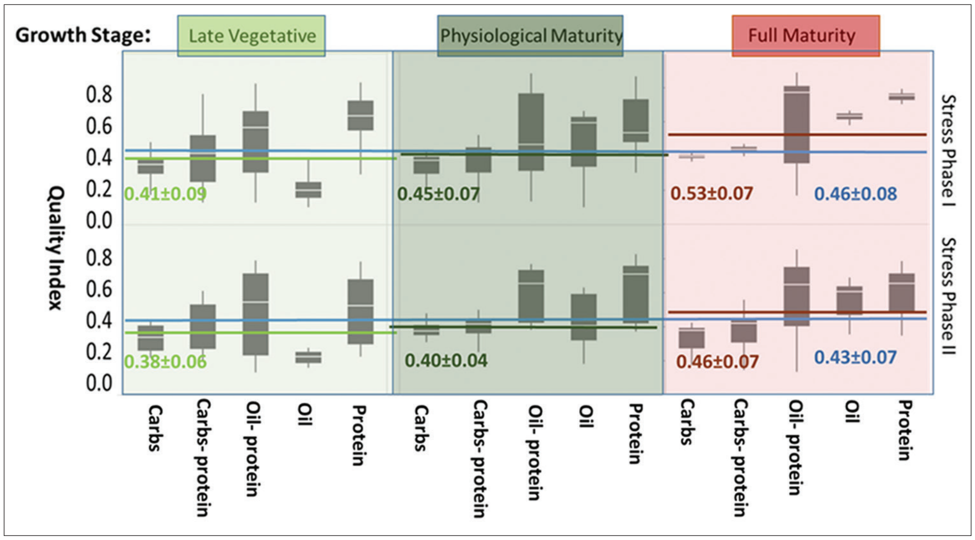


Fig 5. Means (±SD) of quality index averaged for each of two abiotic stress phases, three growth stages of crops producing one or a combination of carbohydrates, protein, and oil.

differences between quality index estimates for crop products within and among stress phases (See Table 5). The level of variation, expressed as the [0.25 to 0.75] range around the median value for each crop prodcuct was largest for oil-protein during all growth stages and under both stress phases; whereas, the smallest was for carbs and carbs-protein at full maturity under stress phas I. All crop products, except oil-protein, expressed larger [0.25 to 0.75] ranges under stress phase II as compared to stress phase I.

Fig 4. Statistical moments and coefficients of quadratic regression equations of plasticity on grain yield for crops producing all products (a) carbs (b), protein (c), oil (d), carbs-protein (e) or oil-protein (f) under two phases of abiotic stress.

Statistical moments, coefficients of RMA regression (scaling exponent, $\alpha_{RMA;}$ and scaling factor, β_{RMA}) in the equation $Y = bX^a$) for quality index as a function of phenotypic plasticity at different levels of organization within two abiotic stress phases are presented in Table 5. No significant changes were observed in mean response quality index as a function of phenotypic plasticity in response to stress phase I (0.57) and II (0.58). Coefficients of RMA regression for quality index as a function of phenotypic plasticity at different levels of organization within both stress phases were statistically significant and their respective R^2 values (0.77 and 0.72) were comparable and reasonably large. However, significant differences between the quality index estimates were found between metabolic pathways, between products and between cultivars within crop species. In addition, significant differences were found between stress phase I and II for carbs (0.62 vs. 0.38), carbs-protein (0.56 vs. 0.43), oil-protein (1.02 vs. 0.74), and protein (0.81 vs. 0.72) crop products. The oil-protein product exhibited the largest quality index estimates under both stress phases, followed, in decreasing order by protein, oil, carbs, and carbs-protein. The quality index estimates of only two crop cultivars (Desi, 0.84 vs. 0.73; and Pioneer, 0.64 vs. 0.48) differed significantly in response to abiotic stress phases.

Most coefficients of RMA regression (scaling exponent, $\alpha_{RMA;}$ and scaling factor, β_{RMA}) were significant. Negative β_{RMA} estimates were found for physiological and full maturity growth stages, all management practices, and the cultivar "Pioneer" (oil-protein) under both stress phases; and for the oil product (phase I), the cultivar "Finch" (oil; phase I), and the cultivar Vital (oil-protein; phase II); however, β_{RMA} for C_3 metabolic pathway was positive but not significant; while β_{RMA} for NS and HS management practices, the oil product, and the soybean cultivar "Vital" (oil-protein product), under phase II were not significant. All α_{RMA} coefficients under both stress phases were positive and significant except for the cultivar "Kabuli" (protein) which was negative. The largest α_{RMA} coefficients were found for the cultivar "Finch" (1.01) under phase I and for the physiological maturity growth stage (1.07) under stress phase II; while the smallest estimates were found for carbs-protein under stress phase I (0.06) and for each of C_4 metabolic pathway and carbs (0.21) under stress phase II. On the other hand, the largest β_{RMA} estimate under phase I and II were found for "Kabuli" chickpea (1.15 and 0.39, respectively); while the respective smallest estimates were -0.15 for the cultivar "Pioneer" (oil-protein) and -0.17 for physiological maturity growth stage. The RMA regression models resulted in a wide range of Jackknifed R^2 estimates; the smallest were 0.18 for carbs-protein under stress phase I and 0.41 for oil-protein under stress phase II; whereas, the respective largest estimates were 0.95 for

Table 5: Statistical moments, coefficients of RMA regression (scaling exponent or slope, αRMA; and scaling factor or intercept, βRMA) in the equation $Y=bX^a$) for standardized quality index as a function of standardized phenotypic plasticity at different levels of organization within two abiotic stress phases (*, significant at p=0.05)

Factor	Sub-factor	RMA test statistics									
		Mean response QI		RMSE		α_{RMA}		β_{RMA}		Jackknifed R^2	
	Stress phase	I	II	I	II	I	II	I	II	I	II
Stress phase	I	0.57		0.08		0.88*		–0.06*		0.77	
	II		0.58		0.08		0.89*		–0.06*		0.72
Metabolic pathway											
	C3	0.64a	0.62a	0.06	0.04	0.74*	0.83*	0.08*	0.02	0.84	0.89
	C4	0.40b	0.39b	0.01	0.01	0.27*	0.21*	0.23*	0.25*	0.32	0.52
Growth stage											
	PM	0.58	0.57	0.08	0.05	0.86*	1.07*	–0.05*	-0.17*	0.77	0.87
	FM	0.56	0.58	0.07	0.08	0.91*	0.87*	–0.08*	–0.04*	0.76	0.70
Management											
	NN	0.56	0.59	0.07	0.08	0.91*	0.91*	–0.08*	–0.07*	0.78	0.75
	HN	0.56	0.59	0.07	0.08	0.89*	0.91*	–0.07*	–0.07*	0.76	0.73
	NS	0.58	0.57	0.07	0.08	0.94*	0.89*	–0.11*	–0.05	0.80	0.73
	HS	0.58	0.57	0.08	0.08	0.82*	0.85*	–0.05*	–0.03	0.74	0.67
Products											
	Carbs	0.62c	0.38c	0.02	0.01	0.08*	0.21*	0.52*	0.25*	0.41	0.52
	Carbs-protein	0.56d	0.43c	0.02	0.01	0.06*	0.45*	0.49*	0.18*	0.18	0.51
	Oil	0.69c	0.62b	0.02	0.01	0.13*	0.32*	0.57*	–0.03	0.24	0.82
	Oil-protein	1.02a	0.74a	0.07	0.04	0.08*	0.41*	0.87*	0.38*	0.43	0.41
	Protein	0.81b	0.72a	0.02	0.01	0.13*	0.60*	0.67*	0.24*	0.67	0.84
Cultivars											
Corn	NK-M808	0.39d	0.42c	0.05	0.04	0.31*	0.27*	0.18*	0.21*	0.48	0.42
	Nokomis	0.40d	0.39c	0.04	0.02	0.23*	0.21*	0.26*	0.25*	0.38	0.51
Chickpea	Desi	0.84a	0.73a	0.04	0.09	0.31*	0.68*	0.48*	0.13*	0.56	0.88
	Kabuli	0.79a	0.75a	0.04	0.05	–0.35*	0.39*	1.15*	0.39*	0.34	0.38
Safflower	Finch	0.70b	0.72a	0.02	0.01	1.01*	0.52*	–0.08*	0.29*	0.95	0.89
	Montola	0.77a	0.73a	0.02	0.01	0.73*	0.75*	0.15*	0.11*	0.79	0.95
Wheat	Bread wheat	0.45d	0.43c	0.04	0.01	0.49*	0.55*	0.17*	0.14*	0.47	0.72
	Durum wheat	0.44d	0.43c	0.05	0.01	0.47*	0.38*	0.18*	0.22*	0.47	0.42
Soybean	Pioneer	0.64bc	0.48c	0.05	0.03	0.63*	0.52*	–0.15*	–0.11*	0.72	0.58
	Vital	0.62c	0.59b	0.04	0.01	0.72*	0.82*	0.21*	–0.01	0.85	0.87

the cultivar "Finch" and 0.95 for the cultivar "Montola", both of which are oil producing safflower cultivars. There were no clear trends in R^2 estimates between both stress phases; numerically, however, some R^2 estimates remained almost stable (e.g., management practices), others decreased slightly (e.g., durum wheat and Pioneer), while those for the cultivars Nokomis, Desi and bread wheat increased.

DISCUSSION

Assessment of experimental design

Abiotic stresses continue to pose a significant challenge for delivering grain of consistent or improved quality in the future due to the complex interactions of several climatic and edaphic variables on grain yield and its quality (Halford et al. 2014; Nuttall et al. 2017). The field experiment carried out during 6 years of fluctuating levels of abiotic stresses subjected 10 cultivars in five crop species to the complexity of resource limitations on crop growth, biomass and grain yield. A range of selection pressures was generated by manipulating the sowing date and plant density (Wang et al. 2017). Physiologically diverse crop plants with the C_3 and C_4 metabolic pathways have been subjected to a combination of management practices which imposed abiotic as well as edaphic stresses during all or half of a 6-year field experiment. Differences among years within abiotic stress phases represent most, if not all, climatic variables, including rainfall amounts and distributions, temperature and length of the growing season. The impact of years as a random factor on variables of interest in the study, at different levels of nesting or interaction with other factors, was significant in 80% of all factor-variable combinations (Table 4).

Multi-trait clustering and association

Phenotypic plasticity is indispensable for crop plant adaptation to changing environments. As resources become more limiting for plant growth and grain yield, the identification of costs and limits to its expression under these emerging environmental conditions is a key research area (Sadras et al. 2016). Historically, agronomists and breeders of field crops considered phenotypic plasticity, which is trait- and environment-specific, as an undesirable phenomenon; however, perspectives on that are changing (Nicotra et al. 2010). However, it is unclear if modern crop breeding and selection under a single productive environment have led to increased or decreased plasticity in traits indirectly correlated with grain yield (Lipiec et al. 2013; Destelfeld et al. 2014). The current study reports on inter- and intra-specific variation in crop phenotypic plasticity under abiotic stress and model its impact on nutritional quality index in physiologically diverse crop species. Crop plants, especially those with C_3 metabolic pathway, besides their ability for functional integration (Weiner 2004; Valladares et al. 2007), they displayed large degrees of plasticity in nutrient concentration under abiotic stresses depending on their biochemical end- product (Figs. 1 and 2).

Considerable changes in plant composition, and therefore, the quality of end-products, can be induced by abiotic stress at all growth stages (Pinson et al. 2012; Kerkhoff et al. 2014); however, different plant tissues or organs may exhibit different responses to such stresses. Crop plants with the C_3 and C_4 metabolic pathways differ in their nutrient status, as documented in this study under both abiotic stress phases (Fig. 1 and Fig. 2) and responded differently to changing stress factors (Obeso 2012; Wang et al. 2017). When crops are grown simultaneously under the same environmental conditions, the risk of allocation being confounded with environmentally-induced variation is minimized (Poorter et al. 2012). Therefore, clustering of, and multi-trait association differences among crops producing different end products within a single abiotic stress phase reflect, to a large extent "true" phenotypic plasticity averaged over large number of both correlated and un-correlated traits (Halford et al. 2014; Rose et al. 2015). The differential effect of stress phases on the association between quality index and phenotypic plasticity can be illustrated by their significant but largely different in magnitude correlation coefficients of 0.71 in stress phase I and 0.32 in stress phase II.

Sources of trait variation

Allocation of biomass by crop plants to the developing grains depends to a large extent on biotic and abiotic environmental variables such as soil water and nutrient contents, as well as on population density (Huang et al. 2010). Obviously, competition for water and nutrients, caused by delayed planting and larger population density, did not only affect allocation of biomass to seed but affected the allometric nutrient allocation as well. Whereas; a reduction of 25% in the duration of developmental growth phases caused by shortened growing season (i.e., NS and HS; Table 1) may have been partly responsible for yield loss by reduction in light interception over the shortened growing season (Lipiec et al. 2013). Abiotic stress triggered by nutrient and water limitations, but not by population density, resulted in larger allocation of nutrients to grains (Huang et al. 2010). Nevertheless, population density may result in an increase, decrease or no change in grain yield (Fig. 4) depending on environmental factors (e.g. water and nutrient availability) (Forsman 2015). The 2-way and 3-way interactions of abiotic stresses with other factors were more important in accounting for differential allocation as was documented in earlier studies (Obeso 2012). Other studies (McCarthy and Enquist 2012) indicated that increasing population density significantly reduced biomass; whereas, competition for water and nutrient resources had negative effects on biomass and grain yield, but their interactions were not significant.

Few studies, where the analysis of variation in nutrient allometric allocation to grains, in response to climate change or to abiotic stress, were considered (Daryanto et al. 2017). The C:N and to some extent C:P ratios emerged as important covariates in partitioning total variance into its components (Table 3); both ratios were closely associated with biomass and grain yield under both biotic stress phases (Fig. 1 and 2). Variation levels of nutrient ratios in this study where well within the range of ratios documented for C:N (5.0 to >100), C:P (<250 >3,500 and N:P (<5.0 to >65.0), but not for N: S (Kerkhoff et al. 2006). The N:S ratio apparently was driven more by changes in seed S than seed N concentration, especially under stress phase II. (Fig. 2); it clustered closely with N:P ratio at a slightly larger clustering distance (stress phase I), in spite of the close association between N and S (Fig. 1). The optimal N:S ratio threshold (22:1) (Salvagiotti et al. 2012), is close to ratios found for carbohydrates and oil-protein products during stress phase I, but larger than the remaining values found under both stress phases (Table 2). Sulfur deficient crop products (large N:S ratio; Table 2) expressed values close to the critical ratio (Salvagiotti et al. 2012; Baxter 2015); whereas, S-rich products (e.g., oil) expressed the smallest value, especially under stress phase II. Nevertheless, the N:S ratio, as an indicator of S status in different crop products, was closely associated with N:P indicating that accumulation of all three nutrients is proportional regardless of the final biochemical seed composition (Salvagiotti et al. 2012; Ciampitti et al. 2013; Ciampitti and Vyn 2013). However, unlike N:P ratio, 44.5% of N:S variation was explained by all random factors, except differences among years within stress phases (Table 4). The N:P ratio may be altered by phytate accumulation in the seed (Sadras and Richards 2014); with P constituting ~75% of phytate, this assumption couldn't be substantiated indirectly on the basis of clustering distances between, N, P, and N:P in the current study (Figs. 1 and 2), and in agreement with earlier findings (Salvagiotti et al. 2012). Dynamics of nutrient ratio (mainly N:P and N:S) were impacted more by the 2- or 3-way interactions than by main factors (Tables 3 and 4), indicating that nutrient accumulation is a complex process under abiotic stresses that can be manipulated to provide quality products under future climate change (Müller et al. 2000; Rose et al. 2015). Unlike C:N ratio, N:P and C:P ratios tend to increase under abiotic stress as crop plants approach full maturity, thus favoring both C and N over P.

Comparative assessment of phenotypic plasticity

Several plasticity indices are available in the literature to quantitatively estimate phenotypic plasticity (Valladares et al. 2007); however, they rendered dissimilar results, with cross-overs in crop species or cultivar phenotypic plasticity rankings. Therefore, standardized phenotypic plasticity estimate based on variance ratio between the stressed and the control treatments have been advocated as a measure of phenotypic plasticity (Sadras et al. 2016). Variability and magnitude of phenotypic plasticity estimates in the current study were triggered by the long abiotic stress treatments (Fig. 4). Phenotypic plasticity estimates based on single trait evaluation may not be as informative as one based on whole plant as an integrated complex phenotype (Forsman 2015). Multiple phenotypic dimensions, presented in this study (Fig. 1 and 2), were analyzed using multivariate statistical methods or composite measures of plasticity at different levels of organization. Those were based on mean values across several traits using dimension reducing statistical procedures.

Although not necessarily adaptive and requires plant energy expenditure, phenotypic plasticity as an environmentally contingent trait expression, was triggered, in this study (Fig. 3) by abiotic stresses during six years of successive experimentation and resulted in alternative phenotypes under different abiotic stresses (Zhang et al. 2008; Halford et al. 2014). Different crop products exhibited large phenotypic plasticity magnitudes (e.g., in response to abiotic stresses and were reflected on the standardized grain yield. Contrary to results based on single phenotypic plasticity estimates (Zhang et al. 2008), when estimated at two successive growth stages (Fig. 3), on average, most products were more plastic at full maturity than at physiological maturity growth stages, presumably due to increased intensity of abiotic stress (Mickelbart et al. 2015).

Grain yield-phenotypic plasticity relationships

Grain yield, as the 'agricultural fitness' indicator of interest to agronomists and producers is increasingly subjected to abiotic stress (Halford et al. 2014). All crop plants express some degree of phenotypic plasticity in facing abiotic stress (Mickelbart et al. 2015). Reproductive allocation (i.e., grain yield) in annual crop plants is the primary target whether under abiotic stress or not. For a given phenotypic trait, such as grain yield, the greater its linkages with other traits, the more limited is its range of variation (Dingemanse et al. 2009). On average, estimated phenotypic plasticity as a function of standardized grain yield ranged from 0.5 to 1.2 and from 0.5 to 1.1 in stress phase I and II, respectively. However, small to large differences between and within crop products (i.e., inter- and intra-specific variation) were found in the relationship between grain yield and phenotypic plasticity (Fig. 4); the smallest (0.5 to 0.6) were for carbs-protein, and the largest (0.7 to 1.4) for oil-protein. These estimates were associated with relatively small R^2 values (ranged from 0.21 to 0.56) as an expression of phenotypic plasticity's prediction by standardized grain yield. Intraspecific differences in plasticity among cultivars (e.g., Desi and Kabuli chickpeas) have been reported (Sadras et al. 2016).

Assessment and prediction of quality index

Maintaining an acceptable nutritional grain quality under abiotic stress is critical for human nutrition, end-use functional properties, as well as commodity value (Nuttall et al. 2017). In this context, grain quality, which is influenced by genetics, management and the environment, was defined as an integrated measure of physical (seed weight and dimensions) and compositional (protein oil, carbohydrates and nutrient contents) properties (Halford et al. 2014; Liu et al. 2016). Several statistical analyses methods have been suggested to formulate and quantify a quality index (Rose et al. 2015). The current study aimed at developing a quality index based on biochemical composition (mainly carbs, oil, and protein) and nutrient contents and their interrelationships under abiotic stress and to compare response of C_3 and C_4 crops to such stresses.

Model II regression, or RMA, has become the standard regression protocol in allometric analyses (Niklas and Hammond 2014) where a mathematical model can be found to fit any nonrandom data set. The scaling exponent (α_{RMA}) estimates for quality index in relation to phenotypic plasticity were predominantly allometric, indicating that abiotic stresses mediated these estimates (Kerkhoff et al. 2006); the only exceptions were the isometric scaling exponent for "Finch" (α_{RMA} = 1.01) under stress phase I and for physiological maturity stage under stress phase II (α_{RMA} = 1.07) (Table 5). Sub-factors (e.g., C3 and C4 metabolic pathway) exhibited statistically different slopes (Table 5), this suggests that different metabolic pathways significantly changed the developmental trajectories of the quality index in response to phenotypic plasticity. On the other hand, sub-factors sharing a common slope but different intercepts (e.g., Pioneer and Vital soybean cultivars) may indicate that these cultivars have different levels of response to abiotic stress. Generally, different slopes and/or different intercepts show that the relationship between quality index and phenotypic plasticity is influenced by sub-factors. Otherwise, equal slopes and intercepts among sub-factors show that the relationship between quality index and phenotypic plasticity remains the same at different levels of a sub-factor (Xie et al. 2012).

CONCLUSION

The ability of field crops to respond to water and nutrient resource availability caused by changing environmental and soil factors (i.e., abiotic stress) is important for maintaining adequate food supply with high nutritional value. Crop plants response to their environment is the sum of all modular responses to local conditions in addition to all interaction effects that can be attributed to phenotypic integration. The concept of phenotypic plasticity was used on data compiled during 6-years of abiotic stress on physiologically diverse crops with different composition of end-products. This concept was used to extend the analysis of the presumed trade-off between crop performance (i.e., biomass, grain yield, quality index and phenotypic plasticity) under abiotic stress as compared to no-stress treatments.

Different crop plants, depending on the species and growth stage, strived to maintain C:N:P:S ratios around a specific value (i.e., stoichiometric homeostasis) in spite of variation in biomass, grain yield and relative availability of nutrients due to abiotic stress. Observed variations in plant biomass, grain yield and C:N:P:S stoichiometry, most probably reflect the combined effects of both plasticity in response to abiotic stresses. Shifts in phenotypic plasticity and quality indices of crops with C_3 and C_4 metabolic pathways, and variation in the scaling exponent, or slope estimates of the five end-products can be used as indicators of crop tolerance to abiotic stress in relation to their quality. More insights are needed into the interdependence of the multitude of traits that crop plants need to optimize under abiotic stress to produce economic yield combined with adequate nutritional quality.

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