



Root to shoot and carbon to nitrogen ratios of maize and soybean crops in the US Midwest

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ARTICLE INFO

Keywords:

Zea mays
Glycine max
 Root traits
 Soil profile
 Carbon
 Nitrogen uptake
 Water table
 Irrigation

ABSTRACT

Root traits are important to crop functioning, yet there is little information about how root traits vary with shoot traits. Using a standardized protocol, we collected 160 soil cores (0–210 cm) across 10 locations, three years and multiple cropping systems (crops x management practices) in Iowa, USA. Maximum root biomass ranged from 1.2 to 2.8 Mg ha⁻¹ in maize and 0.86 to 1.93 Mg ha⁻¹ in soybean. The root:shoot (R:S) ratio ranged from 0.04 to 0.13 in maize and 0.09 to 0.26 in soybean. Maize produced 27 % more root biomass, 20 % longer roots, with 35 % higher carbon to nitrogen (C:N) ratio than soybean. In contrast, soybean had a 47 % greater R:S ratio than maize. The maize R:S ratio values were substantially lower than literature values, possibly due to differences in measurement methodologies, genotypes, and environment. In particular, we sampled at plant maturity rather than crop harvest to minimize the effect of senescence on measurements of shoots and roots. Maximum shoot biomass explained 70 % of the variation in root biomass, and the R:S ratio was positively correlated with the root C:N measured in both crops. Easily-measured environmental variables including temperature and precipitation were weakly associated with root traits. These results begin to fill an important knowledge gap that will enable better estimates of belowground net primary productivity and soil organic matter dynamics. Ultimately, the ability to explain variation in root mass production can be used to improve C and N budgets and modeling studies from crop to regional scales.

1. Introduction

Root traits are key model inputs that operate at field to global scales to predict crop productivity, environmental performance, and biogeochemical cycling. Moreover, there are growing efforts to breed crops for “enhanced root phenotypes” to combat climate change and increase resource use efficiency (Lynch, 2007; Paustian et al., 2016). Knowledge of belowground root traits lags behind knowledge of aboveground plant traits (Laliberté, 2016) because most information about root traits comes from controlled experiments, shallow soil sampling and dated studies (Amos and Walters, 2006; Fan et al., 2016). In addition, crop root traits and their relationships with shoot traits have likely changed with recent developments in plant breeding, climate change, and cropping systems management (Zhang et al., 2013; Gray and Brady, 2016).

Phenotypic variation in maize and soybean root systems presents opportunities to improve cropping systems performance (Barber, 1971;

Gao et al., 2010; Rosa et al., 2019), but only if this variation can be predicted and explained. Maize and soybean cultivars have great tolerance to several stressor factors, such as cold, heat, drought, and poor soil quality (Bandillo et al., 2017; Manchada et al., 2018). Much of this tolerance may be due to root traits that help to cope with these unfavorable conditions. Root growth, particularly during early crop development, helps to mitigate these stressor factors through the uptake of nutrients and water (Lynch, 2007, 2013). However, for this to occur, roots must reach the soil volume where the resources are located (Planet and Lemaire, 2000).

Both maize and soybean root traits are strongly influenced by environmental conditions including soil type, texture and management (Anderson, 1988; Chen and Weil, 2011; Feng et al., 2016; Nichols et al., 2019) water, nutrient and oxygen availability, and microorganism activity (Allmaras et al., 1975; Mayaki et al., 1976; Marschner, 1995; Robinson, 2001; Gallais and Coque, 2005; Fageria, 2013; Florio et al., 2014; Fan et al., 2017), and growth stage (Gao et al., 2010; Comas

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et al., 2013). However, despite this influence of environment, mean root to shoot (R:S) ratios from published reports are often used to estimate root biomass (Hébert et al., 2001; Amos and Walters, 2006). These estimates are widely employed to predict crop production and simulate C budgets in local, regional and global ecosystem models (Bolinder et al., 1997; Xu et al., 2019). Hence, the ability to explain variation in root traits across different environments and managements would improve model predictions.

The relative differences between root and shoot responses to resource variations (e.g., light, water, nutrient, and CO₂) is a central question in the fields of crop ecology and physiology. Partitioning theory (Bloom, 1985) indicates that shoot and root growth are subjected to changes in the relationship between resource supply and demand. Plants promote growth of tissues where the cost of energy returns the greatest benefit in function (White et al., 2016). For example, plants experiencing a low level of nutrient supply are predicted to shift resource allocation toward root growth and nutrient capture rather than carbon fixation. Undoubtedly, these processes affect R:S ratios, and this could potentially explain some proportion of variation in R:S ratios.

In general, the R:S ratio is higher at early growth stages and decreases exponentially through the growing season; values for maize during reproductive growth stages range from 0.02 to 0.40 in glasshouse and 0.02 to 0.25 in field conditions (Amos and Walters, 2006). Soybean displays similar variation across growth stages with values ranging from 0.02 to 0.58 in glasshouse and from 0.08 to 0.31 in field conditions (Gunawardena et al., 1993; Allmaras et al., 1975; Cassman et al., 1980; Amos and Walters, 2006; Fernández et al., 2009; Feng et al., 2016). In addition to this variation across growth stages, there is variation in R:S ratio within growth stages and this variation may represent responses to environmental conditions and sampling approaches (Benjamin et al., 2014).

The carbon to nitrogen (C:N) ratio of roots, which is critical to predict soil organic matter (SOM) dynamics, also varies across environments and growth stages. Root C:N ratio is the primary indicator of crop residue quality, which influences nutrient availability and SOM stabilization (Gentile et al., 2011b; Córdova et al., 2018) in the short- and long-term (Gentile et al., 2011a; Cotrufo et al., 2013; Sprunger et al., 2019). Although low C:N ratios are often assumed to promote nutrient release and SOM stabilization, results are inconsistent (Castellano et al., 2015) and a previous study indicated that the formation and stabilization of SOC is more affected by the quantity of residue inputs and their interaction with soil matrix than the quality of residue inputs (Gentile et al., 2011b). Root traits such as specific root length may be important factors contributing to these inconsistent results. For example, fine roots can result in greater microbial C use efficiency and soil organic matter stabilization than coarse roots (Sprunger et al., 2019).

Root growth and distribution across soil profile are effected by several factors including sampling time, type of vegetation, weather and soil type (Jobbágy and Jackson, 2000; Peng et al., 2010, 2012). Yet, the timing of root measurements varies widely across studies and many measurements of root C:N ratios are made after crop harvest when roots have undergone some decomposition (Dietzel et al., 2016). This may be particularly important for predicting variation in root traits because post-harvest root carbon may be as little as 26 % of total root production for both maize and soybean (Buyanovsky and Wagner, 1986). Together, the strong effects of growth stage, decomposition and environment on root traits demonstrate a critical need for standardized measurements.

Here, we explored several root traits as well as compound root and shoot traits in maize and soybean crops across a wide range of environmental conditions in the Midwest U.S. Corn Belt. Our objectives

were to use a standardized sampling protocol across environments to:

- 1) Quantify the range of variation in root dry weight, length, C:N ratios and R:S ratio values across multiple locations and years.
- 2) Explore possible relationships between root traits, shoot traits and weather.
- 3) Compare data from this study with the literature.

To achieve our objectives, we measured root and shoot traits across 17 maize and 12 soybean site-years including a range of locations that span 55,739 km² and are representative of a major portion of the U.S. Corn Belt. In addition, we reviewed published R:S data to quantify the range of variation and we compared these values with our measured R:S ratios. We hypothesized that relationships between root and shoot traits are strongly affected by growing conditions (site-years). To our knowledge, variation in these traits has not been quantified using a standardized approach for individual crops across multiple site-years.

2. Materials and methods

2.1. Field experiments

Maize and soybean ecophysiological measurements were made across ten sites in the U.S. Corn Belt from 2016 to 2018 (Fig. 1a, b; Table 1). The sites were selected because they represent different climates, soil types, and management practices including irrigation and drainage. All sites except 'Burkey_2017' (see Fig. 1) were managed in an annual rotation of maize and soybean; Burkey_2017 was managed in a continuous maize system (Table 1). Each site and crop included a randomized complete block design with three replicate plots ranging from 360 to 3600 m² (plot size differed across sites but not within an experiment). The Kelley, Nashua and Crawfordsville sites have subsurface 'tile' drainage at ~1.1 m depth while no other sites have artificial subsurface drainage. The Muscatine site was irrigated because crop production is only feasible with irrigation due to high soil sand content (> 90 %); in years 2017 and 2018, 228 and 314 mm of irrigation water were applied, respectively.

We managed all crops, including cultivar selection and agronomic management, according to local practices (Table 1). From the north to south site gradient, maize hybrid maturities ranged from 101 to 115 days and soybean variety maturity groups ranged from 1.9 to 3.4 (Table 1). Soybeans were generally planted one week after maize (Table 1). Plant densities ranged from 8.0–8.8 plants m² for maize and 25–47 plants m² for soybean. In both crops, plant rows were spaced 76 cm apart except Nashua 2016, where soybean plants were spaced 25 cm apart. All maize sites received N fertilizer based on university recommendations (Sawyer et al., 2006); maize in rotation with soybeans received 168–210 kg N fertilizer ha⁻¹ and the continuous maize location (Burkey_2017) received 168 kg N ha⁻¹. Soybean did not receive any N fertilizer. All plots were maintained free of weeds, pests, and diseases. Soil pH and fertility were managed according to university recommendations.

2.2. Soil properties and weather conditions

According to USDA databases (SSURGO and NRCS 2018), soil organic matter (SOM) ranged from 2.9 to 5.1 (g/100 g) in the top 30 cm and plant available water (PAW) ranged from 27 to 125 mm in the 90 cm soil profile. Hourly weather data including temperature and precipitation were recorded at each site. A weather station was located at the border of each field experiment. Across 35 years (1980–2015) and all sites, mean daily (May–August) temperature was ~18 °C and cumulative (May–August) precipitation 516 mm (Iowa Environmental

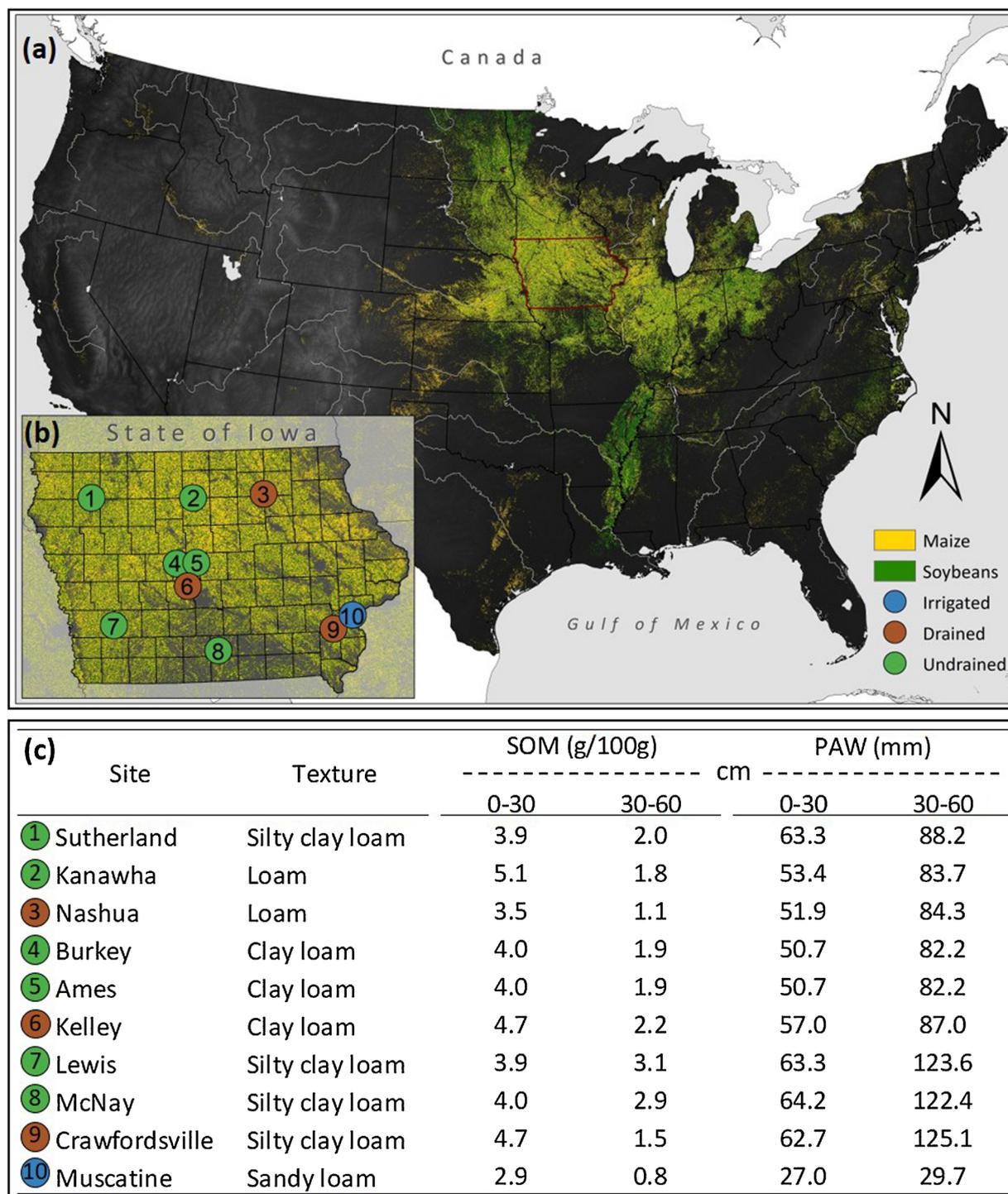


Fig. 1. Location of the experimental sites. Panel (a) displays U.S. maize and soybean planted in 2018 (source [USDA-NASS, 2018](#)). Panel (b) shows all locations included in this study; brown circles represents sites with artificial drainage, green circles represents sites without artificial drainage, and blue circle indicates the irrigated site (site 10). Panel (c) general soil properties (SOM = soil organic matter, and PAW = plant available water). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

[Mesonet Network, 2020](#)). Across site-years in this study, mean daily growing season temperatures differed by up to 4.7 °C; maize at Nashua in 2016 was the coldest at 19 °C and soybean at Crawfordsville in 2016 was the warmest at 23.7 °C. In June-July when maximum root front velocity occurs ([Ordóñez et al., 2018a](#)), the daily maximum temperature difference between site-years was 2.7 °C. Variation in precipitation across site-years in this study was 434 mm; the Kelley site in 2018 received the most precipitation (567 mm) and the McNay site in 2017 received the least precipitation (133 mm; see [Table 1](#)).

Depth to water table, recorded every hour using Decagon CTD-10 sensors (METER Group Inc., Pullman, WA, U.S.A.) in screened wells at each site, typically ranged from 30–200 cm, depending on precipitation, crop stage and soil drainage. Water table data are presented in [Ordóñez et al. \(2018a\)](#) and [Ebrahimi-Mollabashi et al. \(2019\)](#). [Nichols et al. \(2019\)](#) summarized the water table data from all of our studied locations to elucidate the impact over root distribution across soil profile.

Table 1

Management and environmental conditions across the three experimental years. Cultivar growth cycles are in relative maturity (days) for maize and maturity group (MG) for soybean. All sites were maize–soybean rotation system except Burkey_2017, which was a continuous maize system. CV = Coefficient of Variation.

Site / Year	Sowing date	Root sampling date (R2 stage for maize; R5 for soybean)	Sampling position In-row	Sampling position Btw two rows	Cultivar Maturity	Total precipitation from sowing to root sampling (mm)	% Precipitation accumulated during June–July	Average daily temperature from sowing to sampling (°C)	Average daily temperature during June–July (°C)
Maize experiments									
Ames_2016	26-Apr	25-Jul	Yes	Yes	111-day	336.5	158.5	20.6	23.4
Ames_2017*	24-Apr	5-Aug	Yes	Yes	111-day	327.9	114.4	20.1	23.6
Ames_2018	8-May	26-Jul	Yes	NA	111-day	378.5	357.3	22.9	23.4
Burkey_2017*	24-Apr	5-Aug	Yes	NA	111-day	327.9	114.4	20.1	23.6
Kelley_2016	18-May	2-Aug	Yes	Yes	111-day	301.5	208.3	22.2	22.9
Kelley_2017	15-May	12-Aug	Yes	Yes	111-day	254.9	113.1	21.1	22.9
Kelley_2018	17-May	26-Jul	Yes	NA	111-day	484.4	473.7	23.1	22.8
Crawfordsville_2016	13-May	27-Jul	Yes	Yes	111-day	263.5	200.5	22.5	23.8
Lewis_2016	26-Apr	26-Jul	Yes	Yes	111-day	496.3	220.9	20.3	23.5
Nashua_2016	23-Apr	3-Aug	Yes	Yes	105-day	515.6	315.5	19.0	21.9
Sutherland_2016	7-May	4-Aug	Yes	Yes	105-day	265.5	174.2	20.6	22.4
Kanawha_2017	5-May	10-Aug	Yes	Yes	101-day	398.7	251.1	19.6	21.8
Kanawha_2018	18-May	31-Jul	Yes	NA	101-day	430.6	367.3	22.1	22.1
McNay_2017	25-Apr	2-Aug	Yes	Yes	115-day	212.1	52.8	20.9	24.5
McNay_2018	25-Apr	30-Jul	Yes	NA	115-day	346.4	226.9	22.6	24.0
Muscatine-Irrigated_2017	28-Apr	4-Aug	Yes	NA	111-day	444.8	289.6	20.9	23.9
Muscatine-Irrigated_2018	12-May	30-Jul	Yes	NA	111-day	224.3	146.9	23.7	24.1
Average						336.8	61.1	20.5	22.7
CV						35.8	33.4	18.3	9.5
Soybean experiments									
Ames_2016	6-May	8-Aug	Yes	Yes	2.7 MG	281.2	158.6	21.6	23.4
Ames_2017	8-May	5-Aug	Yes	Yes	3.2 MG	266.5	114.6	21.7	23.6
Ames_2018	8-May	18-Aug	Yes	NA	3.1 MG	481.1	357.5	22.9	23.4
Kelley_2016	18-May	8-Aug	Yes	Yes	2.7 MG	322.3	208.2	22.1	22.9
Kelley_2017	30-May	12-Aug	Yes	Yes	3.2 MG	254.9	113.2	22.2	22.9
Kelley_2018	17-May	18-Aug	Yes	NA	3.1 MG	566.8	473.8	21.4	22.8
Crawfordsville_2016	22-May	27-Jul	Yes	Yes	3.1 MG	254.3	200.4	23.7	23.8
Lewis_2016	5-May	10-Aug	Yes	Yes	3.1 MG	410.6	220.9	21.6	23.5
Nashua_2016	26-Apr	3-Aug	Yes	Yes	1.9 MG	515.1	315.8	19.1	21.9
Sutherland_2016	7-May	4-Aug	Yes	Yes	2.2 MG	265.5	174.2	20.6	22.4
Kanawha_2017	9-May	10-Aug	Yes	Yes	2.2 MG	398.7	251.2	19.8	21.8
McNay_2017	9-May	2-Aug	Yes	Yes	3.4 MG	132.8	52.9	22.6	24.5
Average						345.8	60.7	21.6	23.1
CV						37.2	23.1	6.0	3.4

* Sites are close to each other (< 1 km) and thus share the same weather station.

2.3. Above-ground crop sampling procedure

Crop growth was measured destructively from 1.5 m² every other week throughout the growing season. A total of 226 sample events were performed across years, sites, crops, and growth stages. Plants were partitioned into different organs and oven-dried at 65 °C to a constant weight. Subsequently, samples of each plant organ were ground, homogenized and analyzed for total carbon and nitrogen concentrations using dry combustion elemental analysis.

2.4. Below-ground root sampling procedure

In-row and between-row root samples (to a depth of 210 cm) were collected during the grain filling period, which is the R2 growth stage for maize and the R5 growth stage for soybean. We selected these stages in order to capture the maximum root biomass per crop (Kaspar et al., 1978; Amos and Walters, 2006) and avoid root dry matter decomposition or root N remobilization to shoot biomass. We validated that root biomass is maximum at these stages by collecting root samples across 10 times throughout crop growth at Burkey_2017 (Supplementary Fig. 1).

In-row root samples were measured in all site-years. Between-row, root samples were collected in fewer site-years (see Table 1). From

every plot, deep soil cores were extracted using a steel probe (6.2 cm diameter) attached to a hydraulic Giddings machine (Windsor, CO). Cores were divided into sections (0–15, 15–30, 30–60, 60–90, 90–120, 120–150, 150–180 and 180–210 cm) and stored at 4 °C prior to root cleaning following Ordóñez et al. (2018b), which consisted of separating root tissues from soil by using a Hydropneumatic Elutriation washing system (Smucker et al., 1982; Hirte et al., 2017; Gillison's Variety Fabrication).

Following root washing, root tissues were placed in a 24 × 35 cm transparent polymethyl methacrylate tray in about 0.5 cm lamina of water (to avoid overlapping roots) and scanned at 720 dpi using an EPSON V800 scanner. Pictures were analyzed using WhinRhizo Pro software, 2017 (Regent instruments, Inc., Quebec City, QC, Canada) to determine length and other traits. Then root tissues were oven-dried at 60 °C until constant weight to determine dry weight per soil layer. Following drying, the root samples were analyzed for carbon and nitrogen concentrations with dry combustion elemental analysis.

2.5. Calculations

Root mass and length were scaled from soil core depth increments to unit area in two steps. First, we used Eq. (1) and assumed uniform root distribution (mass or length) per layer:

$$Y = \frac{10,000 * x}{(\pi * (\text{probe diameter} * 0.5)^2)} * 10 \quad (1)$$

Where 10,000 is used to convert units from m² to hectares; x is the measured mass or length in grams or cm observed in the depth section; π is 3.14; and probe diameter was 6.2 cm. Second, we summed the values for each depth section from Eq. (1) to a single value and applied Eq. (2), which was recently developed by Ordóñez et al. (2018b) to correct for sampling position biases because root mass and length are greatest in the in-row samples and least in the between-row samples:

$$\text{Weighted average} = \frac{\text{Measured root value} * C}{(1 - \text{plateau}) * e^{(-k * \text{Measured position})} + \text{plateau}} \quad (2)$$

Where measured root value is the value derived from Eq. (1), c, k, and plateau are crop and root trait specific coefficients (see parameter values in the Supplementary Table 1). Eq. (2) was applied to both in-row and between-row samples (separately) and then results were averaged. When only in-row information was available, then outputs from Eq. 2 were used. The measured position refers to the distance from the plant row to the sampling point (in cm).

Root N and C concentrations are reported in this study as averages across the profile. Recent work by Nichols et al. (2019) on the same data indicates little variation of the N and C concentrations across the profile. Total root N and C (kg ha⁻¹) were estimated as the product of concentration and root mass values derived from Eq. (2).

We measured the following shoot traits in this study: 1) grain yield at physiological maturity, 2) total biomass at physiological maturity, 3) maximum biomass achieved at approximate physiological maturity (see below), 4) harvest index (grain yield / maximum biomass; hereafter HI₁), and 5) harvest index by considering grain yield at maturity and maximum shoot biomass plus roots (grain yield / maturity biomass + root mass; hereafter HI₂). We estimated maximum biomass by fitting the crop biomass accumulation data to the beta-growth function (Yin et al., 2003). Among many non-linear models, we used the beta function because it accounts for the biomass decline (due to leaf loss) after a certain point and because maximum biomass is one of the estimated parameters (Archontoulis and Miguez, 2015). Curve fitting was implemented using *nlme* in R software package.

We also calculated the following shoot and root traits: 1) the sum of maximum shoot biomass and the adjusted root mass from Eq. (2), and 2) R:S ratio, calculated in two different ways: the quotients of i) root mass and maximum shoot biomass, and ii) root mass and shoot biomass at harvest (hereafter, R:S ratio and their RN:SN ratios). Finally, we conducted a literature search for field and glasshouse experiments in which roots were sampled from R1 (silking) to R4 (mid grain filling) stage for maize (Ritchie and Hanway, 1982) and from R3 (beginning flowering) to R6 (rapid pod formation) for soybean (Fehr and Caviness, 1977). Articles meeting these search criteria included 17 for maize and 7 for soybean (Supplementary Table 2).

To demonstrate the impact of varying R:S over root mass estimations, we performed a sensitivity analysis to estimate root mass using our shoot biomass and eight R:S values (Supplementary Fig. 3). The R:S values were the calculated mean, median, 3er quartile and 95 % IC values from both our data (Fig. 2) as well as data from the literature (Supplementary Table 2), and values are shown in Supplementary Fig. 3a, b. Root mass was calculated as the product of shoot biomass and the R:S ratio estimates. To display differences between calculated R:S values we then correlated the estimated root mass with the shoot biomass expecting a linear distribution of the points.

2.6. Statistical analysis

Statistical analyses were performed in two ways. Analysis of variance (ANOVA) was used to test for differences in traits (e.g. R:S ratio)

between crops at each site. First, to test for environmental effects across sites (site-year) on crop traits we used randomized complete block analysis with three replications considering sites as random effect factor. Second we used a Split-Plot design with three replications in which crops were the fixed effect and site-years as the random effect. For this analysis, the effect of year was nested with in sites because the degrees of freedom were not the same across locations. This analysis was implemented for those sites in which maize and soybean crops were grown. For this analysis was implemented SAS 9.4 statistical package software (SAS institute Inc., Cary, NC, U.S.A.). Finally, to determine relationships between traits we performed a Pearson's correlation analysis. Illustrations were done in GraphPad Prism 8.1.1 (GraphPad Software, Inc. San Diego, CA, U.S.A.). All the data from all site-years were used.

3. Results

3.1. Above-ground plant traits

Shoot traits varied more across crops (maize vs. soybean) than environments (n = 29 site and year combinations; Table 1). Maize grain yield ranged from 6.8–15 Mg ha⁻¹ and maize biomass from 18 to 29 Mg ha⁻¹ (Fig. 2 and Supplementary Fig. 2). Soybean grain yield ranged from 2.9 to 4.8 Mg ha⁻¹ and maximum biomass from 6 to 11 Mg ha⁻¹. Within each crop, site-year (i.e., environment) had a strong effect on plant traits (Supplementary Fig. 2). The harvest index for maize (at physiological maturity, HI₁) ranged from 0.38 to 0.63 and for soybean from 0.47 to 0.61. Use of maximum shoot biomass to derive HI₁ rather shoot biomass at harvest decreased the HI₁ by 8% in maize and by 23 % in soybean partly because roots are a greater proportion of total biomass in soybean.

3.2. Root traits

In contrast to shoot traits, root traits varied more across environments than between crop species. Maize root mass ranged from 1.2 to 2.8 Mg ha⁻¹, and soybean from 0.8 to 1.9 Mg ha⁻¹ (Fig. 2 and Supplementary Fig. 2). Site-year significantly affected root biomass and length (Table 2). Although environment had a bigger effect on root traits than crop species, maize produced on average, 27 % more root biomass than soybean (p = 0.001, Table 2). This difference between crops was also reflected in the total root length; maize mean root length was 21 % greater than soybean (p = 0.001, Supplementary Fig. 2).

Maize roots had 35 % lower N and 4% lower C concentration than soybean (Table 2). Maize root N concentrations ranged from 0.9 to 1.9 %, while soybean ranged from 1.8 to 2.4 % (Supplementary Fig. 2). The root C concentrations also differed across site-years from 36 to 44 % in maize and from 39 to 44 % in soybean. The mean C:N ratio of maize roots was greater than soybean roots, 30 vs. 20 (Table 2). Maize roots had 12 % less root N (mass per area) than soybean (p = 0.035). Consistent with root N, there was a significant difference in root C across site-years (p = 0.001 and p = 0.014 for maize and soybean, respectively; Table 2). Maize roots produced 25 % more C than soybean (Table 2). Maize root C ranged from 0.4 to 1.2 Mg ha⁻¹ while soybean ranged from 0.3 to 0.8 Mg ha⁻¹ (Supplementary Fig. 2).

3.3. Integrated root and shoot traits

The R:S ratio using maximum biomass (root biomass / maximum shoot biomass) was almost two-fold greater in soybean than maize (p = 0.001; Table 2). Maize R:S ratios ranged from 0.04 to 0.13 with an average and standard deviation of (0.09 ± 0.02), while soybean ranged from 0.09 to 0.26 with an average and standard deviation of (0.17 ± 0.05) (Fig. 2). When R:S ratio was calculated on shoot biomass

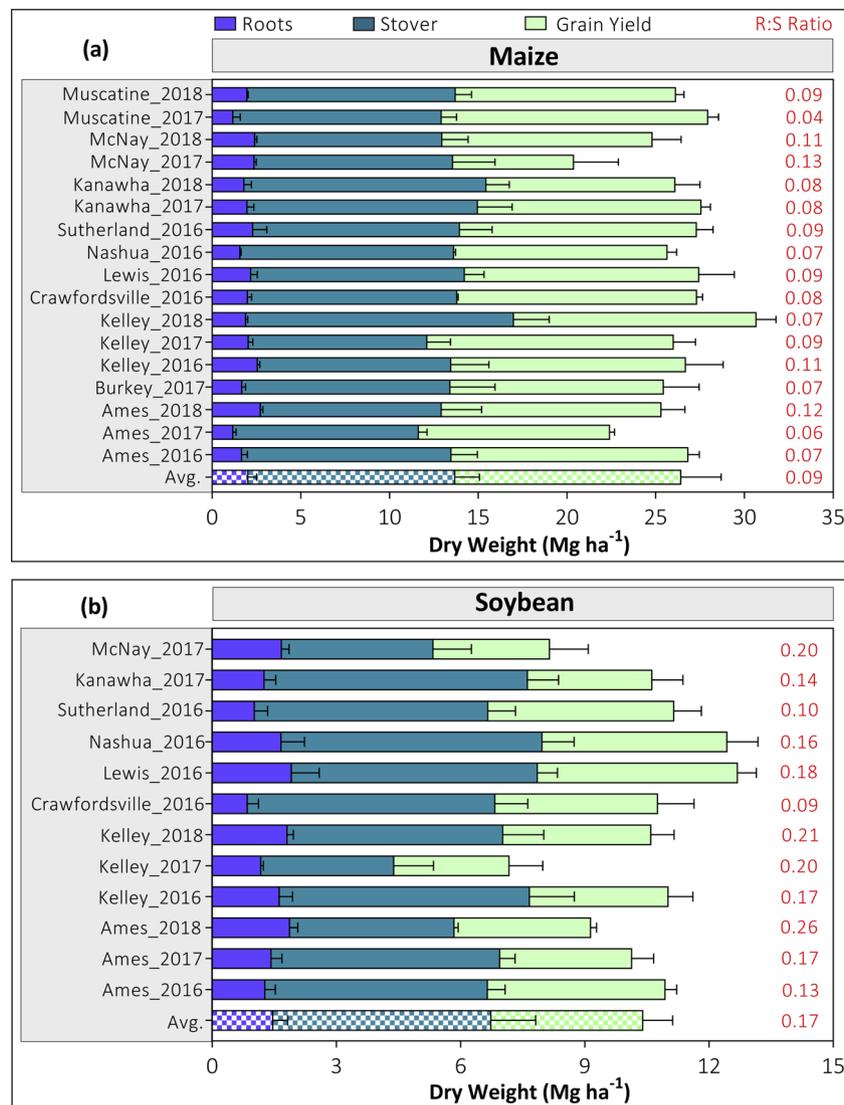


Fig. 2. Maize (a) and soybean (b) biomass distribution: roots, stover (maximum shoot dry weight minus grain yield), and grain yield. Data are means of three replications +/- standard error. Root to shoot (R:S) ratio (root dry weight / maximum dry weight biomass) displayed on the right side of the panel.

Table 2

Analysis of variance for above-ground and below-ground plant traits measured at R2, R5 and maturity for maize and soybean, respectively. The p-value = significant difference according to Tukey's test; CV = Coefficient of Variation and SEM = Standard Error of the Mean.

Variables	Maize (n = 17)				Soybean (n = 12)			
	Mean	p-value	CV	SEM	Mean	p-value	CV	SEM
Root Dry Weight (Mg ha ⁻¹)	2.03	0.001	14.64	0.17	1.48	0.009	22.71	0.19
Root Length (km m ⁻²)	21.42	0.001	16.03	1.98	16.99	0.023	23.32	2.29
Specific Root Length (mm mg ⁻¹)	137.31	0.029	12.67	10.04	157.30	0.001	18.90	10.20
Root Length Density (cm cm ³)	1.80	0.001	15.00	0.15	1.30	0.259	20.00	0.15
Root N Content (%)	1.38	0.001	8.14	0.07	2.13	0.001	6.21	0.08
Root C Content (%)	39.62	0.001	4.03	0.92	41.41	0.001	2.60	0.62
Root C:N Ratio	30.40	0.001	10.13	1.78	19.86	0.005	7.24	0.83
Total Root N Uptake (kg ha ⁻¹)	26.98	0.001	18.01	2.81	30.64	0.018	23.40	4.14
Total Root C Uptake (kg ha ⁻¹)	810.70	0.001	16.89	79.04	607.51	0.014	24.74	86.79
RN:SN Ratio (Root N Uptake / Shoot N Uptake)	0.12	0.001	20.38	0.02	0.13	0.159	29.3	0.03
RN:GN Ratio (Root N Uptake / Grain N Uptake)	0.18	0.001	20.85	0.03	0.15	0.138	30.0	0.04
R:S Ratio (Root / Maximum Dry Weight Biomass)	0.08	0.001	14.53	0.01	0.17	0.001	20.08	0.02
R:S Ratio (Root / Biomass at Maturity)	0.09	0.001	20.01	0.01	0.21	0.001	27.30	0.03
Maximum Biomass (Mg ha ⁻¹)	24.35	0.001	2.34	0.33	8.94	0.001	1.96	0.10
Total Plant Biomass (Roots + Biomass) (Mg ha ⁻¹)	26.38	0.001	2.52	0.35	10.41	0.001	3.61	0.22
Grain Yield (Mg ha ⁻¹) at Maturity	12.69	0.001	11.91	0.87	3.67	0.005	17.49	0.37
Harvest Index (HI; Yield / Biomass at Maturity)	0.52	0.013	12.82	0.04	0.41	0.550	19.78	0.05
Harvest Index (Yield / Total Plant Biomass)	0.48	0.018	12.26	0.04	0.35	0.587	19.66	0.04

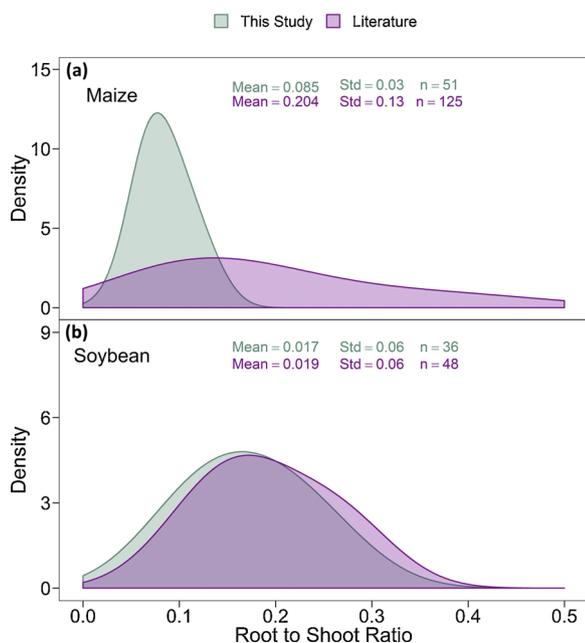


Fig. 3. Density plots comparing root to shoot ratios from this study and field studies reported in the literature (Table 1 and Supplementary Table 2). Std: standard deviation of the mean values.

at maturity (root biomass / shoot biomass at maturity), the values were 0.18 and 0.15 for maize and soybean, respectively. At the site where we measured shoot and root traits over time, maize R:S ratios declined with crop development from 0.27 to 0.08 (see Supplementary Fig. 1).

Published field experiments reported maize and soybean R:S ratios from 0.02 to 0.40 and 0.02 to 0.58, respectively; our R:S data encompass a large proportion of this variation. Our maize R:S ratios values were less than half of published values from the field experiments (Fig. 3; Supplementary Table 2). In contrast, our soybean R:S ratios

values were much closer to published values from field experiments (Fig. 3; Supplementary Table 2). The use of different statistical parameters in the sensitivity analysis had substantial effects on estimated root mass using our shoot biomass and different R:S values (Supplementary Fig. 3).

3.4. Correlations among traits and environmental variables

Pearson correlations between root biomass and plant and environmental variables ranged from +0.86 to -0.35 in maize and from +0.93 to -0.58 in soybean (Fig. 4). Root biomass and length were significantly correlated in both crops ($p < 0.050$; $r > 0.66$). Mean maximum temperature was positively correlated with maize root biomass ($p = 0.020$, $r = 0.57$), while thermal time was positively correlated with soybean root biomass ($p = 0.006$, $r = 0.74$).

Correlations among R:S ratios and environmental variables displayed some similarities with correlations among root biomass traits and environmental variables but also some differences. There was a significant and negative correlation between R:S ratio and total biomass in both crops, however the correlations were weak (Fig. 4). There were also significant positive correlations among R:S ratios and the root C:N ratios (Fig. 4). In terms of environmental variables, maize R:S ratio was significantly correlated with maximum temperature ($p = 0.08$, $r = 0.43$) while soybean R:S ratio was significantly correlated with thermal time ($p = 0.02$, $r = 0.64$).

4. Discussion

The data reported herein can support future work on relationships between root and shoot traits and predictive modeling of crops and soils. A unique aspect of our study was the use of a consistent root sampling protocol. Our previous work showed that measurement methods such as distance from plant row or sampling depth can change root mass estimates two-fold (Ordóñez et al., 2018b). Hence, a standardized protocol is critical to understand the effects of crop and environment on root traits.

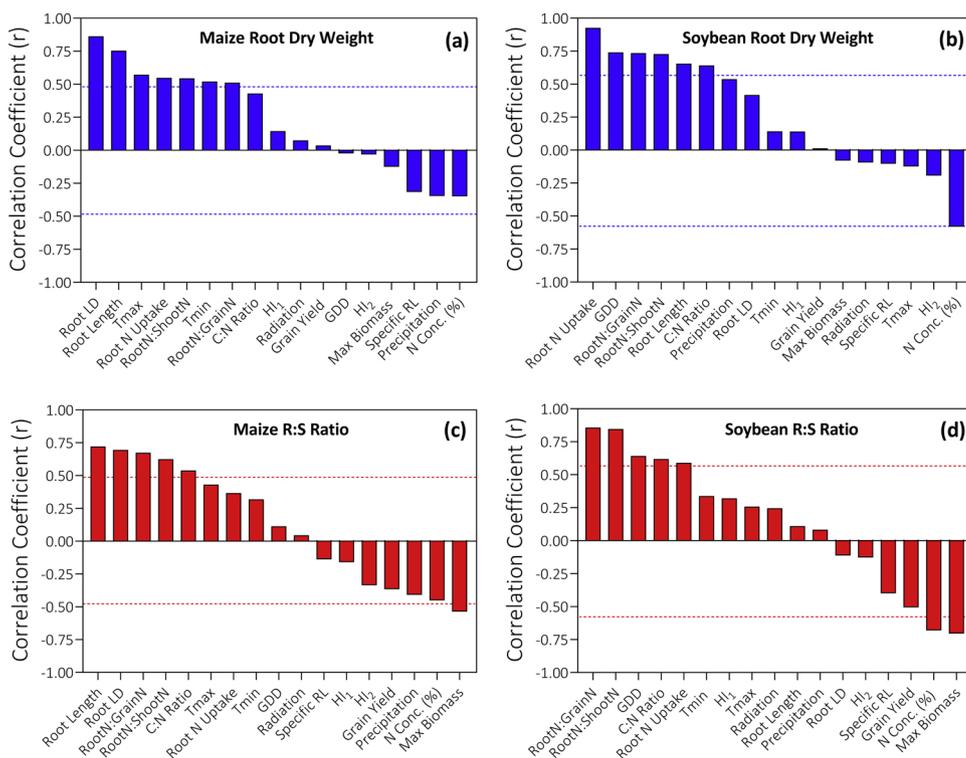


Fig. 4. Pearson correlations (r) between root dry weight panels (a and b) or root to shoot (R:S) ratio panels (c and d), and explanatory variables including Maximum Biomass (kg ha^{-1}); Grain Yield (kg ha^{-1}); Root Length (km m^{-2}); Root Length Density (cm cm^3); Specific Root Length (mm mg^{-1}); Root N Concentration (%); Root C Concentration (%); Root N Uptake (kg ha^{-1}); C:N, RootN:ShootN, RootN:GrainN ratios; Growing Degree Days (GDD); averages daily Tmax and Tmin ($^{\circ}\text{C}$); average daily Radiation (MJ m^{-2}) and accumulated Precipitation (mm) from sowing to sampling. Abbreviations mean: Tmax and Tmin = maximum and minimum temperature; RL = Root Length; LD = Length Density; HI_1 = Harvest Index; HI_2 = Harvest Index (Yield / Root + Biomass DW). Horizontal dotted lines show significant correlations at p -values of 0.05.

Our findings that maize produced 30 % more root mass than soybean, but allocated two-fold less of total biomass to roots (17 % and 9% for soybean and maize, respectively), are consistent with previous studies and known differences in growth strategies (Bolinder et al., 2007; Nichols et al., 2019). These differences could be associated with biological root properties; maize has fibrous roots whereas soybean has a taproot (Mitchell and Russell, 1971; Allmaras et al., 1975; Dwyer et al., 1988). Yet, despite these differences, maize and soybean have no remarkable differences in depth to what both crops can take up water and nutrients (Ordóñez et al., 2018a). And consistent with this result, both crops use approximately the same amount of water (Mayaki et al., 1976).

4.1. Maize and soybean root dry weight and length

In our study, the large effect of site-year on root mass and length was greater than the effect of crop species. This occurred despite the fact that different cultivars were grown among locations to maximize yield potential and reflect practices of local farmers. Moreover, while maize and soybean cultivars differ in terms of phenology across geographies (Table 1), growth related traits, such as radiation use efficiency are similar among cultivars (Archontoulis et al., 2020). Soybean HI values changed more than maize when maximum biomass was used in the calculations and this change was almost certainly associated with greater leaf loss (see Table 2). Previous studies have highlighted the need for reliable root data to predict and understand a wide range of ecosystem properties including soil C sequestration, resource use efficiency, plant nutrition and nutrient loss to waterways (Gerwitz and Page, 1974; Fan et al., 2016; Benjamin et al., 2010). Our work confirms the need for such data. The larger effect of site-year than crop species on root properties clearly demonstrates the importance of an improved ability to predict root traits.

We found strong correlations between root biomass and length in both crops (Fig. 4), which suggests that root biomass can be used as a proxy to estimate root length – if root biomass can be accurately measured or predicted. In particular, correlations between root mass and length were strong within each layer of our sampling from 0–210 cm soil depth ($p < 0.05$, $r^2 = 0.50$ to $r^2 = 0.89$). This finding indicates that shallow root sampling has potential to accurately characterize the complete root system. Knowledge of root length is important because it is often considered to be directly related to the acquisition of water and nutrients (Hamblin and Tennant, 1987; Van Noordwijk and De Willigen, 1991; Lynch, 2013). However, determining root length in addition to root mass is laborious and thus few studies report this trait (e.g. Nichols et al., 2019; Dietzel et al., 2017). Supplementary Table 3 provides equations that relate root mass to length, which can serve as a starting point for future estimations that link crop and environment properties to predict root length.

4.2. Root to shoot ratio

The lack of correlation between root biomass and grain yield or shoot biomass (Fig. 4), demonstrates that shoot biomass – by itself – cannot be used to estimate root biomass across environments. Environment can have different effects on shoot and root processes creating a two-fold range in the R:S ratio (Bloom, 1985), which can lead to substantial over- or under-estimation of root mass (Supplementary Fig. 3). For example, precipitation was positively associated with shoot biomass, but had a small effect on root biomass.

Feng et al. (2016) reported that maize allocates more biomass to roots under fine soil textures. Our data suggest that this result may be due to the effect of texture on water availability. The R:S ratios measured herein were greater in clay soils than sandy soils when water availability was insufficient to meet plant demand. Thus, plants shifted resource allocation in favor of root growth thereby increasing R:S ratio.

In contrast to precipitation, temperature was positively associated

with root biomass and R:S ratio. This finding agrees with a global analysis of roots that found temperature, precipitation and soil texture interact to control root growth and distribution across soil profiles (Jobbágy and Jackson, 2000). In agroecosystems, these patterns can differ with crop species (Sprunger et al., 2019). This indicates that there is a need for more data to develop robust predictive functions that employ plant, soil and weather variables (see, Amos and Walters, 2006; Bolinder et al., 2007, and references therein).

Our results confirm that R:S ratio changes with growth stage (Supplementary Fig. 1). This change likely occurs due to changes in resource supply during annual plant growth and development (Rogers et al., 1996; Amos and Walters, 2006). Our literature review also displayed a large variation on R:S ratios, and this could be related with multiple treatments (low and high inputs) included in the analysis (Fig. 3). Geography may explain why our R:S data differed from the published literature more for maize than soybean. About 70 % of the soybean studies in the literature were from the U.S. including the Midwest region whereas maize studies included much broader geography and growing conditions (Fig. 3 and Supplementary Table 2). Typically, root biomass measurements are made when crops are harvested (e.g. Dietzel et al., 2017) or at physiological maturity (Thom and Watkin, 1978; Tollenaar and Migus, 1984). In this study we followed a different protocol and we measured root properties at maximum standing biomass during the grain filling period to avoid confounding effects of decomposition and nitrogen remobilization from roots. We believe this reduces uncertainty in R:S and root C:N ratios because senescence proceeds at different rates based on climate and environment. Nevertheless, readers should be aware that the time of sampling has a substantial effect on shoot and root biomass and their ratio (Supplementary Fig. 1). Sampling time effects have also been confirmed in perennial crops at the upper Midwest (Sprunger et al., 2019). In addition to growth stage or sampling time, other management factors can also affect shoot and root traits. Although our single N fertilizer rate (168 kg N ha^{-1}) did not allow us to explore the effect of N fertilizer on maize root growth, previous studies demonstrated that N fertilizer can affect R:S ratios (Amos and Walters, 2006; Bolinder et al., 2007). In the case of soybean, soil N availability may affect root growth and fixation but this biological process does not produce dramatic impact on final seed yields (La Menza et al., 2017; Córdova et al., 2019).

Sampling roots by growth stages is likely an important approach to control variation in root measurements and inform a broad range of soil and crop models in terms of calibration and parameterizations. Hence, these data could improve local, regional and global projections of root contributions to ecosystem services such as C sequestration and nutrient acquisition. The relationships developed in this study (see Supplementary Table 3, Fig. 4) can be used to improve prediction of R:S ratio or root mass across environments. Maize root growth was positively correlated with maximum temperature and negatively correlated with precipitation accumulation. Under below-average precipitation, roots are the primary organ that adjusts growth in response to water shortage (Hoogenboom et al., 1987). Alternatively, soybean root growth was positively correlated with thermal time and water accumulation. Thus, soybean root growth appears to be dependent on temperature and less susceptible to excess of moisture than maize.

4.3. Root to shoot ratio sensitivity analysis

Our results demonstrate significant potential for researchers to under- or over-estimate root mass. The use of R:S ratio to estimate root traits was associated with substantial uncertainty for two reasons: 1) large variability among site-years, and 2) comparisons of current vs. past data indicate that modern maize cultivars have 53 % lower R:S ratios (Fig. 3). The decrease in R:S ratio may be due to higher production of shoot biomass in modern hybrids, which results from increased plant densities rather than larger individual plants (Duvick, 2005). Higher yields could potentially be the result of indirect breeding

efforts to reduce the amount of small roots in modern varieties (Zhang et al., 2013).

4.4. The responses of roots and yield to resource availability

The location with the highest grain yield in our study (irrigated, Muscatine see Table 1) had the smallest root mass. In contrast, the location with the lowest grain yield (rainfed, McNay see Table 1) had the largest root mass. At the site with the greatest yield, there was high sand content and irrigation while at the low yield site there was little sand (5%) and the soils were the poorest of all locations (see Fig. 1, panel c). Indeed, the low-yield site is known to have a much higher optimum N rate to corn than other locations in Iowa (Poffenbarger et al., 2017), which suggest soil constraints to resource uptake by the crop (Poffenbarger et al., 2018). We suggest that, at the low-yield site, the plants allocated more dry matter below ground in an effort to acquire more resources from a very limited pool and thus the higher root mass in this location. The allocation of more dry matter below ground likely came at the cost of lower shoot dry matter and thus the lower grain yields.

These results also demonstrate that root biomass is not necessarily positively associated with higher rates of water and nutrient uptake. This is because resource uptake depends not only on root mass and architecture, but also on resource availability in time and space (Hammer et al., 2009; Lynch, 2013; Eissenstat, 1992). These complex interactions indicate that meaningful root parameters can fluctuate independently from shoot growth; neither are they dependent on soil moisture content, except the maximum root depth trait, which, within Iowa, is largely controlled by water table depth (Ordóñez et al., 2018a; Nichols et al., 2019). Thus, researchers should be cautious when using allometric models to estimate root parameters (Fan et al., 2016), particularly, in those studies aiming to quantify soil carbon inputs as well as nutrient and water uptake.

4.5. Root C and N

We found that a considerable amount of nitrogen and carbon can be stored in the roots of maize and soybean (Table 2). However, our results for N might be slight overestimates of the total N that remains in root systems at harvest, which can be reduced due to N remobilization to grain (if there is a need) and other plant organs. Our goal in this study was to quantify the maximum amount of C and N that can be stored in roots rather than what is left at crop harvest. Thus our root C:N values were lower than those reported by Dietzel et al. (2017) where the roots were collected three weeks post-harvest. This is not surprising because at that time we would expect at least some decomposition prior to post-harvest senescence (crops are typically harvested 2–3 weeks after physiological activity ceases) and decomposition would increase root C:N ratio.

5. Conclusion

The larger effect of site-year than crop species on root traits highlights the need for better predictive models of root properties. Lower maize R:S values in this study compared to the literature may have one more explanations. Estimation of maize root traits may be more sensitive to methodological differences than soybean and much higher rates of yield increase over time for maize than soybean may result in greater alteration of maize roots due to breeding. Indeed, for maize, the location with the greatest root mass had lowest shoot mass, which is consistent that historical yield gains may be altering root traits (Zhang et al., 2013). This highlights a major challenge for the future modeling

of crop and soil processes that estimate root properties from above-ground measurements such as yield. The relationships we explored between roots, shoots and the environment can be used to improve predictive models and guide future research.

CRedit authorship contribution statement

Raziel A. Ordóñez: Conceptualization, Methodology, Formal analysis, Visualization, Investigation, Writing - original draft. **Sotirios V. Archontoulis:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition. **Rafael Martinez-Feria:** Investigation, Writing - review & editing. **Jerry L. Hatfield:** Writing - review & editing. **Emily E. Wright:** Investigation. **Michael J. Castellano:** Conceptualization, Writing - review & editing.

Declaration of Competing Interest

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

Acknowledgments

This work was sponsored by the Iowa State University Plant Sciences Institute faculty scholars program, Iowa Soybean Association, Foundation for Food and Agricultural Research (#534264), Iowa Crop Improvement Association and USDA-NIFA Hatch projectIOW10480. We sincerely thank Gerasimos Danalatos for creating the map used in Fig. 1; Emily Marrs, Cooper Smith and Oluwakorede Olugbenle for assistance in sample collection and processing.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.eja.2020.126130>.

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