



Exploring the Association Between Inherent Soil Nutrient Availability and Crop Responses Following Long-term Cessation of Fertilizer Inputs in a Wheat–Maize Cropping System

Weimo Zhou^{1,2,3} · Syed Tahir Ata-Ul-Karim¹ · Naoki Moritsuka⁴ · Yoichiro Kato¹

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Abstract

Intensive agriculture relies mainly on the injudicious application of fertilizers. The importance of inherent soil fertility is often ignored owing to the complexity of the relationship between crop productivity and soil properties in the field with continuous fertilization. Here, our goal was to improve the understanding of long-term crop responses to soil nutrient availability. This study was one component of long-term nutrient management experiments conducted from 1993 to 2018. Field receiving standard fertilization before 2007 was divided into fertilized and non-fertilized plots. Fertilizer application was suspended in non-fertilized treatment since 2007 for 11 years, but control treatment continuously received standard fertilization (252–164–281 kg ha⁻¹ year⁻¹ of N–P–K) from 1993 to 2018. Crop biomass and N uptake decreased by 29–69% and 28–76% of standard fertilization in wheat and maize, respectively from 2008 to 2011, and then stabilized at 10–41% and 31–73% of standard fertilization in wheat and maize, respectively, from 2012 to 2018. Spatial analysis of crop growth and soil characteristics showed that grain yields of both species after cessation of fertilization were associated with total and available soil N ($r=0.62$ – 0.79). The large within-field yield variation (42–52%) after 3 years of suspended fertilization resulted from a slight (9%) variation in soil N availability. Cessation of fertilizer affected vegetative growth of wheat and reproductive growth of maize and both species showed different determinants of the yield formation processes under low soil fertility.

Keywords Long-term experiment · Fertilizer management · Nutrient availability · Inherent soil fertility · Crop rotation

Weimo Zhou and Syed Tahir Ata-Ul-Karim equally contributed as co-first authors.

✉ Yoichiro Kato
ykato@g.ecc.u-tokyo.ac.jp

¹ Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi, Bunkyo, Tokyo 113-8657, Japan

² University of Chinese Academy of Sciences, Beijing 100049, China

³ Key Laboratory of Land Surface Pattern and Simulation, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

⁴ Graduate School of Integrated Arts and Sciences Agriculture, Kochi University, 200 Otsu, Monobe, Nankoku city, Kochi 783-8502, Japan

1 Introduction

Global crop production has kept pace with ever-increasing food demand mainly due to the consumption of synthetic fertilizers (Shahzad et al. 2019; Tilman et al. 2002). However, excessive fertilization leads to lower grain yield, poor nutrient-use efficiencies, nutrient imbalance, destruction of soil structure, and deterioration of soil productivity (Bei et al. 2018; Han et al. 2015; Zhang et al. 2018). Sustainable crop production requires appropriate land management for improving and sustaining soil fertility. However, the complexity of relationships between soil fertility and crop productivity makes the accomplishment of this goal challenging in modern agriculture. Consequently, understanding the association between crop yield, crop nutrient demand, and soil nutrient supply capacity is imperative to develop more eco-friendly and sustainable management strategies for modern cropping systems.

A low-input system ensures crop production by cutting down the dependency on inorganic fertilizers by optimizing

other management practices (Hossard et al. 2016). However, relying solely on organic amendments can lead to plant nutrient deficiency as a consequence of decreased or imbalanced levels of readily available nutrients in the soil (Chen et al. 2018). Intra-field spatial heterogeneity in soil indigenous nutrients, edaphic conditions (moisture and temperature), and external inputs (Chen et al. 2015; Tiftonell et al. 2013) can considerably affect crop nutrient uptake and photosynthesis. Besides, the application of inorganic fertilizer often masks the underlying effects of indigenous soil nutrient supply and its interactions with plant growth (Venkatesh et al. 2017; Wang et al. 2018a, b). Accordingly, field experiments are often confounded by the interactions among multiple possible causes of the observed effects and difficulty in identifying the key relationship between soil nutrients and crop growth. Therefore, understanding the role of indigenous soil nutrient supply on crop nutrient demand requires monitoring of crop productivity without external inputs.

Long-term experiments have played important role in agricultural decision-making (Venkatesh et al. 2017). However, the injudicious input rate and non-synchronization between the nutrient availability and crop demand during the crop growth period are the major challenges for sustaining crop yield and soil fertility on a long-term basis (Sacco et al. 2015). Besides, the impacts of fertilizer suspension for evaluating its long-term effects on crop growth and soil properties also remained unexplored, as most studies focused on the short-term effects of fertilizer suspension on the variation of crop growth, yield, and soil properties (von Arb et al. 2020; Wickings et al. 2016).

Crop models offer an alternative to long-term experimentation. However, sequential simulations using crop models often fail to predict the gradual change in soil properties over years. A study simulating maize growth over 50 years of continuous cultivation without fertilizer application using the CERES-Maize model overestimated the yield (Liu et al. 2011). The variation in soil properties over time makes it difficult to explain the effects of soil nutrients on crop yield in long-term low-input cultivation. Consequently, the exploration of changes in crop yield without any external fertilizer input in a long-term experimental study would improve our understanding of the effects of inherent soil fertility on crop growth. Therefore, we hypothesized that slight intra-field spatial variation in soil characteristics can greatly affect crop productivity in low-input long-term cultivation.

Maize and wheat cultivation in the rotation is one of the major cropping systems worldwide. The intensive maize and wheat rotation together with inappropriate nutrient management lead to nutrient mining from the rhizosphere. Crop nutrient demand is determined by the soil's inherent nutrient supply, nutrient application (rate and time), and previous crop (Zhang et al. 2015). However, fertilizer application in

intensive rotation systems generally ignores the carryover effect of fertilizers on the succeeding crops. Consequently, exploring the coupling effects of inorganic fertilizer application and residual soil fertility on a long-term basis is imperative to work out crop nutrient requirements to sustain crop productivity and soil fertility in resource-intensive agriculture.

This study endeavored to fill these research gaps by elucidating the long-term evolution of crop productivity after the suspension of fertilizer application in maize-wheat rotation in fields that had previously received continuous standard fertilization for more than 10 years. Additionally, the spatial variability in crop growth and soil characteristics was also investigated to reveal the relationships between soil nutrient status and crop yield.

2 Materials and Methods

2.1 Site Description

The long-term field experiment was conducted from 1993 to 2018 at an upland farm of the Institute for Sustainable Agroecosystem Services, The University of Tokyo, Japan (35°43'N, 139°32'E). The average annual precipitation, daily mean temperature, maximum temperature, minimum temperature, and mean solar radiation at the Tokyo Meteorological Station located 20 km from the site were 1570 mm, 16.5 °C, 20.4 °C, 13.2 °C, and 12.8 MJ m⁻², respectively (Suppl. Fig. S1). The soil was volcanic ash (Andosol) and is characterized as a Typic Melanudand according to USDA Soil Taxonomy, with sand:silt:clay content of 51:34:15. The soil properties before the start of the experiment (1993) were: pH 5.8; EC 0.075 mS cm⁻¹; total N, 4.4 g kg⁻¹; available N 91 mg N kg⁻¹; Bray no.2 P, 393 mg P₂O₅ kg⁻¹; total carbon, 59 g kg⁻¹; and a bulk density of 0.77 g cm⁻³. Surface runoff was not likely to occur owing to the flatness (slope < 0.1%) of the experimental field.

2.2 Setup of the Long-term Experiment and Treatments

This study was one component of long-term experiments that have compared fertilization (organic vs. inorganic fertilizers) in maize-wheat rotation systems (Kato and Yamagishi, 2011). The experimental field (17 m × 60 m) received standard fertilizer applications without any organic amendment such as straw or manure. The soil properties of the plough layer before the setup of the long-term experiment (2007) were: pH 5.93; EC 0.077 mS cm⁻¹; total N, 3.7 g kg⁻¹; available N 93 mg N kg⁻¹; and Bray no.2 P 380 mg P₂O₅ kg⁻¹. The annual nitrogen-phosphorus-potassium (N-P-K) application rates for wheat were 84–55–94 kg ha⁻¹ from 1993 to

2018, and those for maize were 168–109–187 kg ha⁻¹. The N-P-K fertilizers were broadcasted as ammonium sulfate, triple superphosphate, and potassium chloride. The experimental field receiving standard fertilization in the long-term experiment before 2007 was divided into two zones (fertilized and non-fertilized) before maize plantation in 2007 each zone having an area of 510 m² (8.5 m × 60 m). The standard fertilization treatment (control) continuously supplied the same N-P-K rates used in previous years, whereas the other treatment received no fertilizer. It was not possible to establish a fully randomized complete block design. Instead, we established four 8.5 m × 15 m transects (plots) for long-term monitoring of both treatments. We also established 2.0-m-wide boundaries between the fertilization and non-fertilization treatments to minimize interactions between the fertilizer regimes.

Aboveground plant residues were removed from the field after harvest. Soil preparation was done by using the same tillage method (a moldboard plow to a depth of 30 cm, followed by harrowing to a depth of 15 cm). The soil properties of non-fertilization treatment after the harvest of the last season crop (2017) were: pH 6.12; EC 0.049 mS cm⁻¹; total N, 1.8 g kg⁻¹; available N 20.2 mg N kg⁻¹; Bray no.2 P 287 mg P₂O₅ kg⁻¹.

Maize (*Zea mays* L. “KD720” from 1993 to 2008 and “KD731” from 2009 to 2018) was grown from June to October. Wheat (*Triticum aestivum* L. “Kinunonami” from 1993 to 2009 and “Satonosora” from 2010 to 2018) was grown from November to June. Maize was sown at 79,300 plants ha⁻¹, with a row spacing of 71 cm. Wheat was drill-sown in rows separated by 18 cm at a seeding rate of 80 kg ha⁻¹. The other crop management practices (weeds, pests, and diseases) followed local recommendations.

2.3 Investigation of Spatial Variability in Crop Growth and Soil Properties

Eleven micro-plots (1.5 m × 1.2 m) were established in 2010 for maize and wheat during 2009–2010, 2010–2011, and 2016–2017 to investigate the spatial variability in maize and wheat crop growth (crop biomass, crop N uptake, grain yield, harvest index, number of grains, grain weight, and grain N concentration) and soil properties (EC, pH, total N, inorganic N, available N) in non-fertilization treatment. The sampling was conducted from an area of 0.8 m² at 5.5-m intervals in a line that ran along the midpoint of each plot (fertilized and non-fertilized), with sampling locations marked with signs to allow repeated measurements at each position. The micro-plots were established at a distance of 0.8 m from the sampling locations marked with signs to examine the effect of N application on the spatial variability in crop yield. Thus, the micro-plot setting was like a kind of an equal spacing sampling to collect the soil and

crop samples in the non-fertilization treatment, and thus to further analyze the spatial variation in these micro-plots. Besides, each micro-plot was fenced with 30-cm plastic boards inserted to a depth of 10 cm in the soil one day after wheat sowing, and 140 kg ha⁻¹ of N was basally applied as ammonium sulfate; we refer to this as the wheat topdressing 2011 treatment in the non-fertilization treatment.

2.4 Sampling and Measurements

Aboveground biomass and N content of wheat and maize were determined at physiological maturity from an area of 2.77 m² in maize and 1.58 m² in wheat from 2008 to 2018 for the long-term monitoring in fertilization and non-fertilization treatments, except in 2011, 2015, and 2018 for maize due to typhoon-induced destruction of the crop. Plant samples were oven-dried at 80 °C for 72 h to determine the dry weight. The dried samples were ground and the N content was determined with an NC analyzer (Sumigraph NC-90A, SCAS, Tokyo, Japan). The variability of biomass and N uptake in the wheat–maize rotation system during the study period was calculated by dividing the biomass and N uptake of non-fertilization treatment by those of control (standard fertilized treatment). The critical N dilution curves of wheat (%Nc = 5.5DM^{-0.44}) and maize (%Nc = 3.40DM^{-0.37}) were used to calculate plant N status at harvest for maize and wheat, respectively (Justes et al. 1994; Plénet and Lemaire, 1999). The nitrogen nutrition index (NNI) of wheat and maize was calculated by dividing actual plant N concentration by plant critical N concentration.

Grain yield, yield components, and crop growth from 2009 to 2011 were also determined in fertilization and non-fertilization treatments. During the crop growth period, leaf area was measured at anthesis from an area of 1.0 m² (maize) and 0.4 m² (wheat) from each plot with a leaf area meter (LI-3100, LI-COR, Lincoln, NE, USA). We randomly selected 3 maize plants and 10 wheat plants as a subsample and separated them into stems and leaves followed by a measurement of the green leaf area. The fraction of radiation intercepted by the canopy was also measured at 7 to 10 days interval with a linear ceptometer (LP-80, Decagon Devices Inc., Pullman, WA, USA). The radiation-use efficiency (dry matter growth per unit radiation intercepted), specific leaf N (leaf N per unit leaf area), and specific leaf area (leaf area per unit leaf mass) were also calculated. Plants were harvested from an area of 1.58 m² from each plot to count ears (maize) and spikes (wheat) at maturity. Then grain weight and grain number were determined after hand-threshing of a subsample of 5 ears and 50 spikes at maturity. The grain yield and grain weight were expressed at 0% grain moisture content. The differences in yield component and growth characteristics of maize and wheat after 3 years were compared using the equation of (*Non-fertilized-control*)/*control*.

Soil chemical properties of the topsoil layer (20 cm) were determined before sowing in the non-fertilization treatment from 2008 to 2010. Soils were collected with a soil core sampler (DIK-106B, Daiki Rika Kogyo, Saitama, Japan; 40 mm in diameter) at five positions from each plot and mixed to have a composite sample. The composite samples were then air-dried and sieved to pass through a 2-mm mesh. Total C and N were determined by using the dry combustion method. Soil electrical conductivity (EC) and pH (H₂O) in a 1:5 (w/v) soil: water mixture was measured with a glass electrode. Inorganic N equaled the total of NH₄⁺ and NO₃⁻ measured by the indophenol method (Mulvaney, 1996) and the Cataldo method (Cataldo et al. 1975), respectively. The content of mineralizable N (as available N) was obtained by subtracting the content of initial inorganic N in the soil from the content of inorganic N after anaerobic incubation at 30 °C for 4 weeks (Moritsuka et al. 2013). Available P was determined by the Bray No. 2 method (Bray and Kurtz, 1945). Grain yield, biomass, and crop N content were determined as described above at maturity from an area of 0.8 m² from each micro-plot avoiding the border rows to eliminate edge effects for the spatial investigation in non-fertilization treatment (2010 and in wheat in 2009–2010, 2010–2011 and 2016–2017) and topdressing treatment (2011).

2.5 Statistical Analysis

The statistical differences between treatments were tested by using paired *t*-tests. The coefficient of variation measured

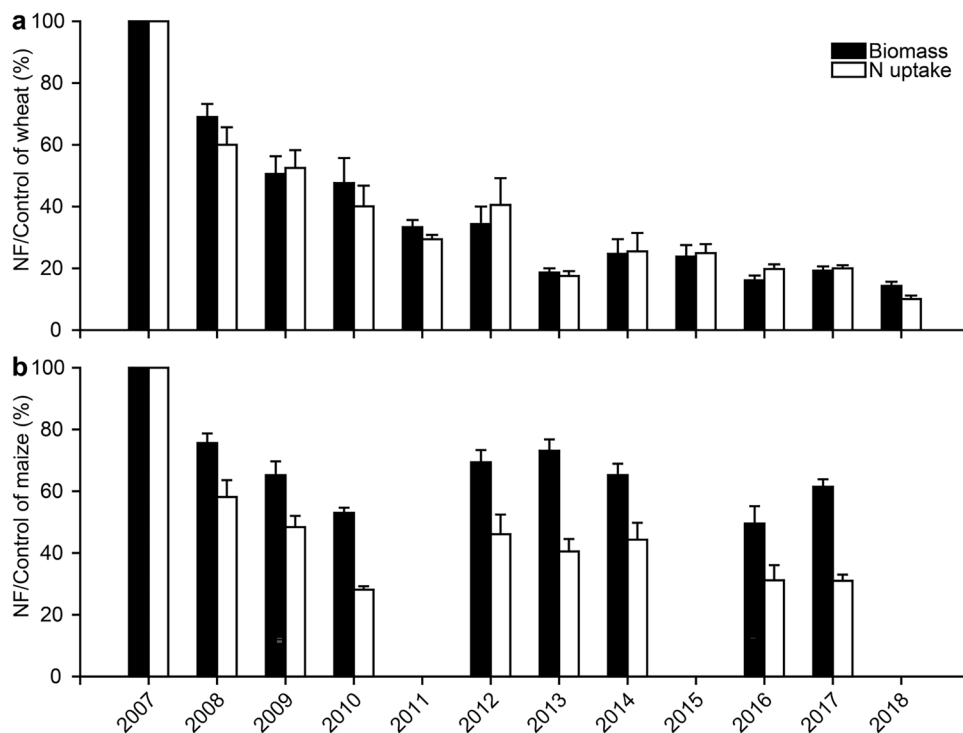
($CV = s/\bar{x}$, where *s* and \bar{x} is the standard deviation and means of crop growth and soil properties across 11 micro-plots, respectively) for determining the spatial variability of crop growth and soil properties. Additionally, the Pearson correlation coefficient was used to quantify the correlation relationship between crop and soil characteristics. The statistical significance of the correlation relationship was tested by using *t*-tests. The data analysis and plotting of graphs were conducted using Matlab R2020a.

3 Results

3.1 Assessment of Crop Growth and Nitrogen Status for 11 Years After the Suspension of Fertilization

The average aboveground biomass and N uptake were 14.95 t ha⁻¹ and 168 kg ha⁻¹ and 14.72 t ha⁻¹ and 163 kg ha⁻¹ under standard fertilization from 2007 to 2018 in wheat and maize, respectively (Suppl. Fig. S2). The biomass and N uptake in wheat under the non-fertilization treatment decreased to approximately 30% of the control during the first 4 years (2008 to 2011) after the suspension of fertilizer application (Fig. 1a). Subsequently, the values remained stagnant at 10 to 25% of the control from 2013 to 2018. The decrease in N uptake in maize under the non-fertilization treatment was similar to that in wheat during the first 3 years (Fig. 1b).

Fig. 1 Crop biomass and N uptake of wheat (a) and maize (b) in the non-fertilization treatment (NF) from 2007 to 2018 (mean ± SE, *n* = 4). Values in NF relative to control were shown



However, the values did not continue to decrease and remained at 31 to 46% of the control from 2012 to 2017. Maize also maintained a higher proportion of the biomass than wheat after suspension of fertilizer application. Moreover, the variations of nitrogen nutrition index (NNI) in wheat and maize under control and non-fertilization treatment during all growing seasons were shown in Fig. 2. The NNI values in control ranged from 0.62 to 0.93 and 0.59 to 1.27 in 2008–2018 for wheat and maize respectively. Conversely, the NNI under non-fertilization treatment was lower with values ranging from 0.28 to 0.54 and 0.36 to 0.60 within the study period for wheat and maize, respectively. There was a bi-phasic long-term transition of crop growth after the suspension of fertilization: a period of rapid decline (2008 to 2011) and a period of stability with minor fluctuation (2012 to 2018). However, there was no obvious variation of NNI in both crops after suspension of fertilization during the study period, yet maize demonstrated a higher fluctuation of NNI than wheat.

Fig. 2 Nitrogen nutrition index (NNI) of wheat (a) and maize (b) in control and non-fertilization treatment (NF) from 2008 to 2018 (mean \pm SE, $n=4$)

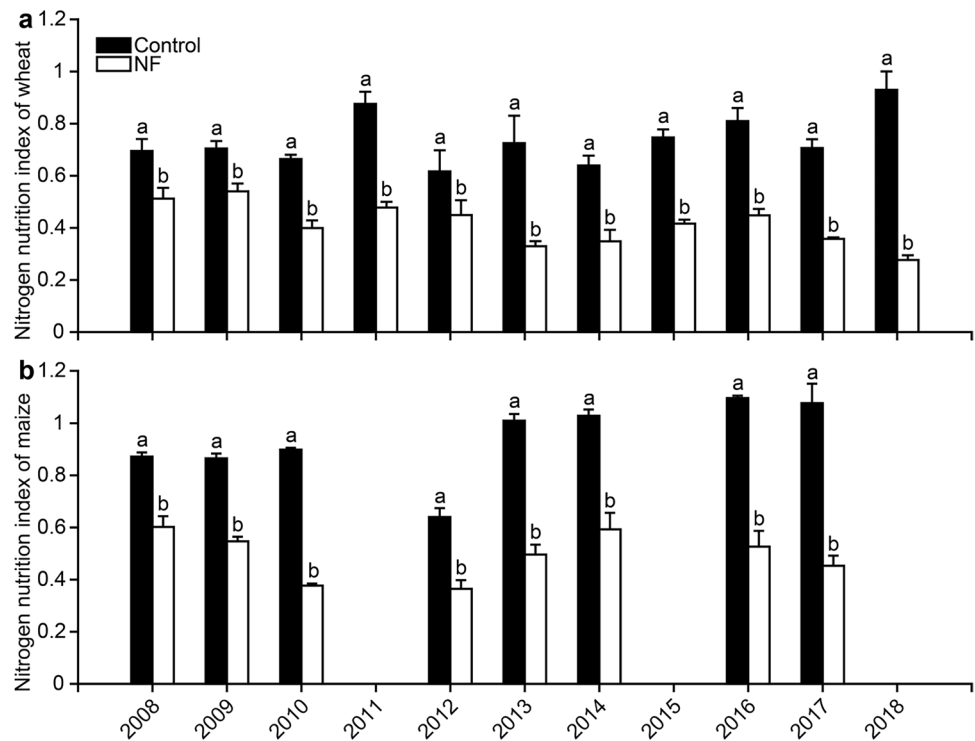


Table 1 Soil chemical properties in the non-fertilization field

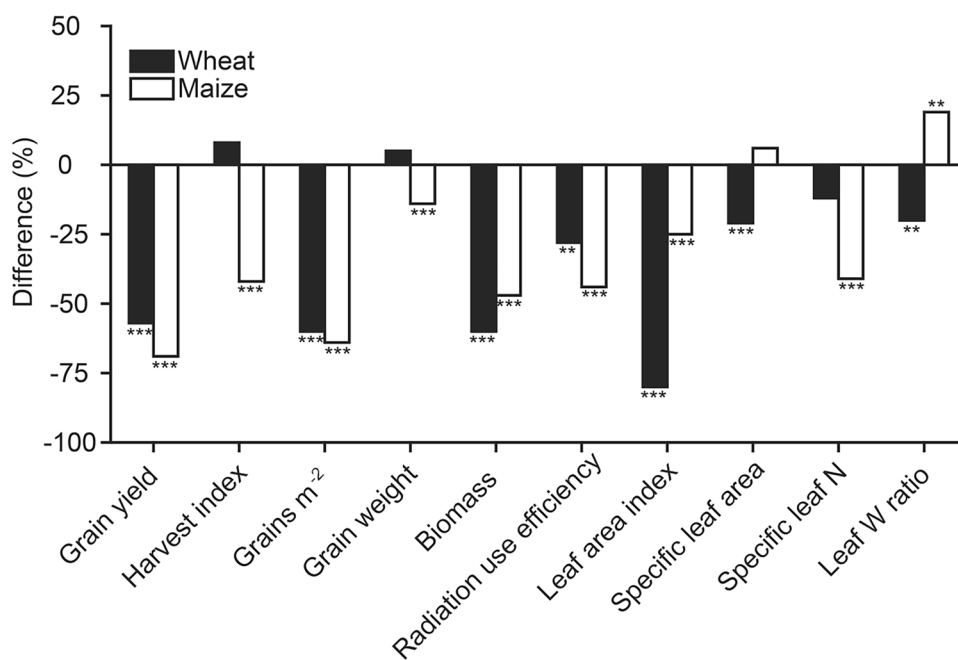
Month, year	pH (H ₂ O)	Electrical conductivity (mS cm ⁻¹)	Total nitrogen (g kg ⁻¹)	Inorganic nitrogen (mg kg ⁻¹)	Available nitrogen (mg kg ⁻¹)	Bray no.2 phosphorus (mg kg ⁻¹)
June, 2008	6.28	0.073	3.4	21.6	68	330
June, 2009	6.06	0.067	2.7	14.5	51	370
June, 2010	6.07	0.061	3.7	11.3	44	320

3.2 Assessment of Crop Growth and Soil Characteristics Within the First 3 Years After the Suspension of Fertilization

Soil chemical properties were measured from 2008 to 2011 to characterize the period of rapidly decreasing crop productivity under the non-fertilization treatment (Table 1). Soil EC and pH (H₂O) decreased slightly during the second (2009) and third (2010) years after the suspension of fertilization. However, the decrease in inorganic and available N after 3 years of suspended fertilization was large: 24 to 48%. Conversely, the available P and total N contents did not decrease. The soil chemical properties in the control treatment are shown in Suppl. Table S1.

Crop yield and other agronomic characteristics were also examined in the third year after the suspension of fertilization (Fig. 3; Suppl. Table S2). There were significant differences between maize and wheat in the plant and yield responses to decreasing soil fertility, with the greatest difference for the harvest index (Fig. 3). Grain yield, grain number, and biomass

Fig. 3 Difference in yield component and growth characteristics of maize and wheat after 3 years of suspended fertilization as compared to the control. Maize, 2010 summer; wheat, averaged data of 2009–2010 and 2010–2011 winter. The significance differences were tested by paired *t*-tests. Double and triple asterisks represent $P < 0.01$ and 0.001 , respectively



decreased by 47 to 69% in maize (2010) and by 57 to 60% in wheat (2009–2010, 2010–2011) as compared to 2007. The harvest index and grain weight of maize decreased by 42% and 14%, respectively, whereas wheat showed non-significant increases during the same period. The radiation-use efficiency and specific leaf N decreased more in maize than in wheat. Conversely, the specific leaf area, leaf weight ratio, and leaf area index decreased more in wheat than in maize.

3.3 Within-Field Variability in Crop Growth and Soil Characteristics in the Non-fertilization Treatment

Spatial variations in crop N uptake, grain yield, and grain number among the 11 micro-plots in the non-fertilized field

ranged from 30 to 52% in 2010 and 2011 (Fig. 4; Suppl. Table S3). Wheat and maize showed opposite trends in biomass and harvest index (larger spatial variation of biomass and smaller spatial variation of harvest index in wheat, while a smaller spatial variation of biomass and larger spatial variation of harvest index in maize). Compared with crop growth, the spatial variations in soil inorganic N (16%), available N (9%), and total N (6%) were small, whereas soil pH showed negligible variation and EC showed low variation (4%) (Table 2). Besides, the spatial variation in crop N, grain yield, and grains m⁻² in wheat decreased to 6% and 9%, when the variation in N availability was minimized by topdressing N fertilizer. The spatial variation in these parameters decreased greatly in 2017 as compared to those in 2010 (Fig. 4).

Fig. 4 Variation in crop growth of wheat (a) and maize (b) at different positions ($n = 11$) within the non-fertilization field. CV, coefficient of variation; W, wheat; M, maize; TD, top-dressing of N (14 g N m^{-2}) in micro-plots

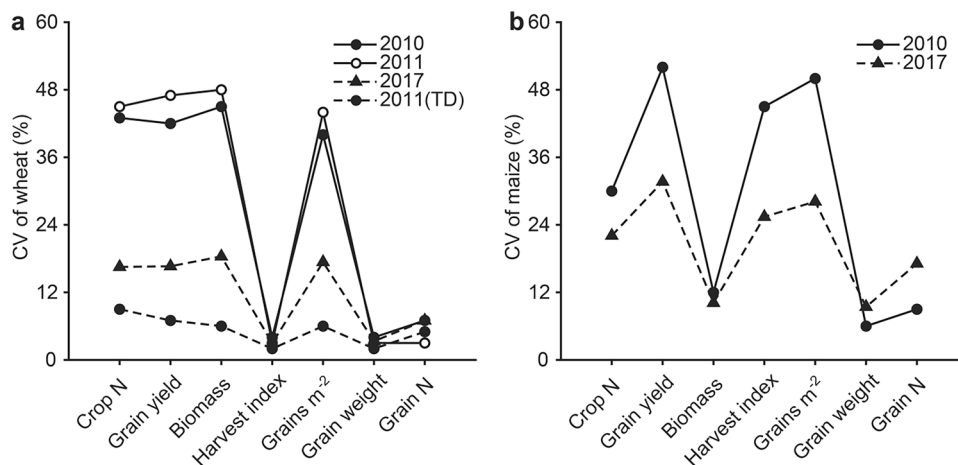


Table 2 Range and coefficient of variation of soil chemical properties at different positions ($n = 11$) in 2010 and 2011 in the non-fertilization field

	Electrical conductivity (mS cm ⁻¹)	pH (H ₂ O)	Total nitrogen (g kg ⁻¹)	Inorganic nitrogen (mg kg ⁻¹)	Available nitrogen (mg kg ⁻¹)
Range	0.057–0.066	5.99–6.08	3.8–4.5	13.1–23.0	45–60
CV	4%	0.4%	6%	16%	9%

CV coefficient of variation

Significant and positive correlations between yields in the same and consecutive years and between the corresponding N uptake values in maize and wheat were observed among the 11 positions in the non-fertilized field (Suppl. Fig. S3a, b). However, there was no correlation in a given crop between 2010 and 2011 (Suppl. Fig. S3c, d). When ammonium sulfate was top-dressed to minimize the variation in N availability, the correlation between wheat yield and N uptake was not significant (Suppl. Fig. S3e, f). The total N and available N in the soil after 3 years of suspended fertilizer were significantly and positively correlated with crop yield and N uptake (Table 3).

4 Discussion

Crop growth and yield responses are regulated by soil indigenous nutrient supply, and the relationships between them can be employed for nutrient management. The interactions between crop and soil variables under fertilized conditions make the understanding of spatial variability regulating crop responses challenging. Therefore, we attempted to evaluate long-term crop productivity after the suspension of fertilizer application in a wheat–maize rotation.

The transition of crop productivity under non-fertilization treatment in this study was in consensus with a study stating that crop and soil responses to added nutrients remain 6 years after discontinuation of long-term treatments (Liu

et al. 2020). The rapid decreases in biomass and N uptake under the non-fertilization treatment in the first 4 years (2008 to 2011) might be associated with the rapid consumption of soil inorganic N and labile organic N, which were directly taken up by crops or were quickly mineralized by soil microorganisms (Sebilo et al. 2013). Meanwhile, the stagnation of N uptake in the non-fertilized treatment from 2012 to 2018 can be explained by a stable equilibrium between mineralization of insoluble soil N (N supply) and crop N uptake (N demand). Besides, an equilibrium between a labile organic N pool produced by immobilization of mineral N during residue decomposition as a consequence of plant senescence may also exist. Therefore, N and P fertilizer applications are considered imperative for sustaining crop productivity and soil fertility (Erisman et al. 2008). Their excessive use has resulted in altering N:P stoichiometry and soil properties such as pH and EC, which in turn pose multiple impacts (size, structure, diversity, and activity) on soil microbial community (Janes-Bassett et al. 2020). The stable P status within this period was attributed to a change in N:P stoichiometry due to the cessation of fertilizer application. The minor decline in soil EC was also linked with a decline in fertilizer salts due to cessation of fertilizer application and leaching of existing salts to lower soil layers due to irrigation or rainfall. This decline in soil EC due to the lowering of fertilizer salts in the rhizosphere was in consensus with a previous study (Ata-Ul-Karim et al. 2020). The decline of soil pH despite the cessation of fertilizer application might

Table 3 The correlation coefficient between soil properties and crop productivity in the non-fertilization field

	Electrical conductivity	pH (H ₂ O)	Total nitrogen (g kg ⁻¹)	Inorganic nitrogen (mg kg ⁻¹)	Available nitrogen (mg kg ⁻¹)
Grain yield					
Maize, 2010	0.28	0.10	0.62*	−0.25	0.66*
Wheat, 2010	0.42	0.25	0.72*	−0.03	0.79**
Wheat, 2011	0.35	0.37	0.70*	−0.03	0.67*
Wheat, 2011, TD	−0.15	−0.44	0.27	−0.52	0.04
Crop N uptake					
Maize, 2010	0.31	0.36	0.58	−0.07	0.56
Wheat, 2010	0.52	0.25	0.75**	−0.01	0.76**
Wheat, 2011	0.35	0.38	0.71*	−0.01	0.70*
Wheat, 2011, TD	−0.17	−0.25	0.26	−0.44	0.19

TD top dressing of N. Single and double asterisks represent $P < 0.05$ and 0.01 , respectively

be attributed to the decomposition of soil organic matter and crop residues. The decline in crop productivity was primarily attributed to the soil N status as a variation in soil P, pH, and EC were negligible. The amount of plant-available N after four years of suspension of inorganic fertilizer application should be largely determined by the activities of soil microorganisms due to the depletion of residual fertilizer before 2008. Soil microbial communities play an imperative role in sustaining rhizosphere functioning due to their regulatory role in nutrient cycling and decomposition of organic matter. The soil microbial community responsible for soil N mineralization (Wang et al. 2018a, b; Zeng et al. 2016) could become less active as a consequence of continuous use of inorganic fertilizers under control (Zhao et al. 2016), while their activity becomes higher under low fertilization condition.

The fluctuation of NNI (less than the optimum value of 1) under control treatment in wheat from 2008 to 2018 suggested that the rate of N supply was not sufficient for reaching non-limiting N growth conditions, which is common practice in Japan to maintain grain quality and avoid crop lodging. The decline of NNI in wheat under non-fertilization treatment was attributed to a large decrease in soil N availability from 2008 to 2018. Conversely, better N nutrition status of maize under control and non-fertilization treatment as compared to wheat were attributed to their different genotypic and eco-physiological responses. The decrease in NNI of both crops during the investigated period under non-fertilization treatment was attributed to the progressive decline in soil N mineralization as a consequence of the long-term cessation of fertilizer application. However, the lower fluctuation in maize as compared to the wheat crop might potentially be associated with the fluctuation of soil water status and higher temperature in the summer period.

The significant positive correlation observed between maize and wheat yields in the same and adjacent years suggested that species and climatic conditions they experienced during the growth period, as well as soil available N, were potentially responsible for the decline in crop growth under the non-fertilization treatment. N fertilizers can continue to provide N to crops in the years after fertilization after being bound to soil organic matter (Sebilo et al. 2013). Soil available N is derived mainly from the decomposition of soil organic matter (Zhao et al. 2016). The differences in inherent soil resources and previous field management appear to be the main causes of spatial variability in soil available N (Tiftonell et al. 2013). Our results revealed that the spatial variability in yield and N uptake after 3 years of non-fertilization was significantly associated with soil N availability, and the variability decreased in 2017 thereafter as a result of continuous N removal by the crops. Interestingly, we found that even a slight change in soil properties, particularly in N

fertility can lead to high variation in crop yield and N uptake in a field that has received only inorganic fertilizers.

The lower reduction in biomass accumulation by maize than wheat under the non-fertilization treatment can be attributed to the higher physiological N-use efficiency (biomass accumulation per unit N uptake) in a C₄ crop (maize) than in a C₃ crop (wheat) (He et al. 2007). Additionally, the rate of soil N mineralization is influenced by seasonal variations in temperature (Miller and Geisseler, 2018). Higher N uptake in maize than in wheat was potentially attributable to the higher mineralization rate of soil organic N to inorganic N under the warm summer conditions during maize growth. The ability of maize to uptake soil N from the deeper layers because of its deep root system might also be responsible for higher N uptake in maize than in wheat (Zhao et al. 2006).

Nitrogen deficiency in maize can result in a smaller grain number as a consequence of the reduced emergence of distal silks (Lemcoff and Loomis, 1994). The reduction in grain number and grain weight in maize which are determined after anthesis (Mayer et al. 2012), might have caused a yield reduction under low soil fertility. N deficiency in wheat during the vegetative period reduced spike number (data not shown) (Fischer et al. 1993), which led to reduced grain number at maturity. Previous studies also confirmed that grain number in wheat is strongly associated with pre-anthesis N availability (Duan et al. 2018; Oscarson, 2000). We speculate that the two crop species have different determinants of the yield formation processes under low soil fertility. Maize continues to accumulate biomass under nutrient stress, but the growth of its reproductive organs is susceptible to nutrient deficiencies, causing a large reduction in the harvest index. Conversely, wheat is likely to reduce its vegetative growth and spike number, and thus its sink size (grain number), thereby improving the growth of its reproductive organs and stabilizing its harvest index.

Our results confirmed different growth adaptations in maize and wheat to low soil fertility. An increase in the specific leaf area (the formation of thin leaves) and the leaf weight ratio (the high allocation of dry matter to leaves) in the maize crop resulted in a smaller reduction in the leaf area index at the expense of decreased specific leaf N, which was in consensus with previous studies (Lemaire et al. 2008; Vos et al. 2005). This suggests that maize seeks solar radiation by maintaining coverage of the ground area at the expense of decreased N concentration per unit leaf area under low soil fertility. Conversely, the smaller decrease of the specific leaf N of wheat as compared to maize contributed to the maintenance of radiation-use efficiency under low soil fertility but sacrificed the light-capture capacity (a larger decrease of specific leaf area and

leaf area index). Our results suggested that the differences between wheat and maize in their agronomic performances under low soil fertility were intrinsic to the genetic responses of the two species (Lemaire et al. 2008). These results provide a clear eco-physiological explanation for the dynamic adjustments of maize and wheat to low-input or infertile conditions during crop growth and yield simulation.

5 Conclusions

Long-term monitoring of crop productivity demonstrated that soil inorganic N and available N decreased immediately after the suspension of fertilizer application in a conventional maize-wheat cropping system, whereas soil pH, total N, and available P changed little during the study period. The decrease in soil available N due to the suspension of fertilizer application was the dominant factor responsible for the reduction of crop productivity. Cessation of fertilizer affected the vegetative growth of wheat and the reproductive growth of maize, and both species showed different determinants of the yield formation processes under low soil fertility. Additionally, a relatively small variation in soil nitrogen availability can lead to a high variation in crop yield in the non-fertilization field. The judicious soil management to increase the soil's nitrogen-holding capacity through measures such as organic matter application will be critical to developing more eco-friendly sustainable agriculture.

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Author Contribution Weimo Zhou: data curation, formal analysis, writing – original draft.

Syed Tahir Ata-Ul-Karim: data curation, writing – original draft.

Naoki Moritsuka: methodology, investigation, data curation.

Yoichiro Kato: conceptualization, supervision, funding acquisition, writing – review & editing.

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Declarations

Competing Interests The authors declare no competing interests.

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