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RESEARCH ARTICLE

Developing functional relationships of corn growth and developmental responses to nitrogen nutrition for modeling

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Abstract Nitrogen (N), one of the essential mineral elements, is involved in many biochemical processes and ultimately closely relates to agronomic yield. Our ability to monitor N concentrations in plants through direct tissue sampling or remote sensing has rapidly evolved as technology has advanced. However, functional relationships between morphological and physiological processes and tissue N have yet to be widely published and are needed to advance precision and predictive agricultural technologies further. Therefore, an experiment was conducted to determine the relationships between tissue N concentration and corn (*Zea mays* L.) morphological and physiologic characteristics. Plants were grown in pots under optimal conditions in sunlit controlled-environment chambers but with varying N supplies. Plant growth, developmental, and physiologic properties were monitored weekly. Shoot N content differed among treatments and declined over time for all treatment levels. Photosynthesis declined as N content decreased, but these decreases were largely non-stomatal limiting. Reductions in N content were due to declining chlorophyll and N balance index values and increasing flavonoids and anthocyanins. Stem elongation and leaf expansion were highly sensitive to declining N content. Below the soil surface, root growth and development rates fell and held a quadratic relationship with N content. Roots were less sensitive at low N stress levels than plant growth above the soil surface. The functional relationships produced from this study could help update crop simulation models and apply them to emerging precision agriculture technologies.

Keywords Corn, modeling, nitrogen, photosynthesis, root growth, shoot growth

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1 Introduction

Global agricultural production is critically limited by abiotic factors (National Academies of Sciences, Engineering, and Medicine, 2019). Nitrogen (N) availability and uptake support crop growth, development, and agronomic yield (Glass, 2003). Accounting for approximately 1%–5% of total plant dry weight, N is the often most abundant mineral element within plant tissues and is involved in many complex biochemical processes (Muratore et al., 2021). However, many environmental and management factors influence the availability of this crucial nutrient throughout the crop-growing season. The availability of N throughout the entire life cycle plays a significant role in determining agronomic yield. For example, Ciampitti and Vyn (2012) demonstrate that corn grain yield is closely related to total plant N uptake measured at physiologic maturity.

Most agronomic management strategies for non-legume crops include the application of synthetic or organic N, and N inputs on US farms doubled from 1961 to 2000 (Howarth et al., 2002). In 2018, the United States planted approximately 36 million hectares of farmland with corn (*Zea mays* L.). An average of 162.5 kg·ha^{-1} N was applied in 97% of surveyed fields planted with corn in the US, representing a total of 5.4 billion kg of N (Sumner et al., 2021). Unfortunately, N fertilizer application rates greater than the uptake capacity are subject to loss and can adversely affect the environment through runoff and leaching. Such losses also detrimentally impact economic stability through high input costs and poor returns on investment (Glass, 2003; Raun and Johnson, 1999; Jaynes et al., 2001; Kingston-Smith et al., 2006; Mengel et al., 2006; Jägermeyr et al., 2020)

Although N inputs increased following the introduction of synthetic fertilizers, N use efficiency, or the amount of grain produced per unit of N applied to the soil, has not increased at the same rate (Lassaletta et al., 2014). A recent global study estimated that plants do not directly recover more than half of the supplemental N applied to soil (Omara et al., 2019). The application of excess fertilizer that fails to be utilized by plants may lead to adverse physiologic (Gerik et al., 1998; Reddy and Matcha, 2010) and environmental and economic impacts (Glass, 2003; Raun and Johnson, 1999; Jaynes et al., 2001; Kingston-Smith et al., 2006; Mengel et al., 2006). Advanced fertilizer application methods and nutrient management strategies are being introduced at the nexus of remote sensing, precision agriculture, and plant physiology to increase N-use efficiency (NUE), economic returns on investment, and realized yields. Although it is possible to sense N levels in plant tissue remotely (Sumner et al., 2021; Reddy and Matcha, 2010; Raper et al., 2013; Zhao et al., 2005), knowledge gaps still need to be filled to determine the best optimal N application rates and timing based on real-time plant N status paired with future estimates of N demand. Plant growth modeling will be a crucial addition to current precision agriculture technology to support management decisions relating to precise and efficient N applications.

Extensive research has determined the importance of N on plant growth and development. Previous studies have established that plants primarily use N to produce and maintain leaves for photosynthetic carbon (C) fixation into functional biological molecules (Broadley et al., 2000). An extensive review by Radin and Mauney (1986) described many plant responses to N deficit. They suggested that lower N content results in lower photosynthetic rates, slower leaf expansion, and an altered response (largely stomatal) to N stress. Nitrogen deficiency reduces root hydraulic conductivity and the water potential of expanding leaves. As a result, N-deficient leaves cannot maintain the adequate turgor needed for growth, thereby restricting mesophyll and epidermal cell expansion (Radin and Boyer, 1982). Other studies suggest that the stunted growth of plants under N deficiency is primarily due to restricted leaf expansion rather than lower rates of photosynthesis (Ciompi et al., 1996). However, few studies have systematically quantified the relationships between plant N concentration and plant growth, development, and physiology.

Plant root access to N varies temporally and spatially due to soil heterogeneity and dynamic microbial conversions, affected by agronomic practices and environmental conditions (Muratore et al., 2021). Thus, root morphology and growth are critical determinants for the uptake of immobile and mobile nutrients in the soil (Peng et al., 2010). Some studies highlight the essential role of root structures in N acquisition, although few have quantified the relationship between plant N concentration and root morphology. Effective nutrient acquisition depends on the size of the root system and the structural deployment and distribution of roots throughout the soil profile. Root architecture is a primary determining factor of the capacity of plants to uptake essential nutrients and moisture from the soil to sustain plant growth (Li et al., 2006). Robinson (2001) suggests that root length per unit of soil volume determines a plant's ability to uptake nitrate from the soil. In addition, strong relationships have been observed between the amount of root biomass and soil moisture depletion (Craine et al., 2003). Therefore, quantifying the relationship between plant N concentration and root morphology during early vegetative growth stages will help unravel how N status could affect a plant's future ability to uptake nutrients and moisture during critical growth stages occurring later in the growing season.

The objectives of this study were to 1) quantify the effects of different N supplies on the N concentration, growth, development, and physiologic characteristics of corn during early growth stages and 2) quantify the functional relationships held between plant N concentration and growth, development, and physiologic characteristics.

2 Materials and Methods

2.1 Experimental facilities

A study was conducted at the Mississippi Agricultural and Forestry Experiment Station's Environmental Plant Physiology Laboratory, Mississippi State University, MS, USA (33°28′N, 88°47′W). Experiments were conducted using Soil-Plant-Atmosphere-Research (SPAR) units (available at Mississippi State University website). These facilities allow plants to grow under natural solar radiation while controlling environmental conditions, including temperature, carbon dioxide (CO_2) concentration, soil moisture, and nutrient levels. Each SPAR unit contains a soil bin, a 1.27-cm Plexiglas canopy that allows 97% of photosynthetically active radiation to pass, a heating and cooling unit, and an environmental monitoring and control system. SPAR unit operation and control details have been described previously (Reddy et al., 2001). For this study, the soil bin within each SPAR unit housed 30.5 cm height × 15.2 cm width polyvinyl chloride (PVC) pots. These pots contained a drain hole and 2.54 cm of pea gravel (500 g) on the bottom of the pot to facilitate drainage. The remainder of each pot was filled to the top with pure, fine sand, particle size less than 0.3 mm). Each pot was connected to a drip irrigation system to supply nutrient solutions. Plants were irrigated three times a day (0800 h, 1200 h, and 0500 h) through an automated and compter-controlled drip irrigation system. The amount of nutrient solution delivered to each pot was based on the amount of evapotranspiration measured on the previous day (Reddy et al., 2001) to each pot. Evapotranspiration rates expressed on a ground area basis (L H_2O $m^{-2}\cdot d^{-1}$) throughout the treatment period were recorded in each

SPAR unit at which the condensate was removed by the cooling coils at 900-s intervals by measuring the mass of water in collecting devices connected to a calibrated pressure transducer (Mckinion and Hodges, 1985; Reddy et al., 2001; Timlin et al., 2007).

2.2 Plant materials

Seeds of corn hybrid Agrigold A6659 (Agrigold Inc., St. Francisville, IL) were sown into 30 pots per SPAR unit. Four seeds were sown in each pot and subsequently thinned to one plant per pot after seedling emergence. Environmental conditions for each SPAR unit were set to 30°C/22°C (day/night), 70% relative humidity, and 420 ppm CO_2 to create optimal growing conditions for seedling emergence. Pots were initially watered three times per day for 60 s per irrigation event with full-strength Hoagland's nutrient solution (Hewitt, 1953) to ensure adequate nutrient and moisture levels for rapid seedling emergence.

2.3 Treatments

Upon emergence, five treatments were imposed to create different N concentrations within the corn plants. These treatments were imposed by altering standard Hoagland's nutrient solution (macronutrients consisting of 0.7094 g·L $Ca(NO_3)_2$, 0.2817 g·L KNO_3, 0.2742 g·L $MgSO_4$, and 0.058 g·L KH_2PO_4 $^{-1}$ and micronutrients consisting of 0.0305 g·L EDTA, 0.0098 g·L NaCl, 0.0033 g·L $MnCl_2$, 0.0031 g·L H_3BO_3, 0.0004 g·L $CuSO_4$, 0.0005 g·L $ZnSO_4$, and 0.0002 g·L $(NH_4)_6MO_7O_{24}$) to contain different N concentrations by substituting $CaCl_2$ for $Ca(NO_3)_2$, thus reducing the quantity of nitrate. All nutrients other than N were maintained at the same relative concentrations as the control (full-strength) nutrient solution. The five treatments included full-strength Hoagland's nutrient solution (control, 100% N) and four reformulations containing 60%, 20%, 10%, and 0% of the N in the control solution. The five treatments were assigned randomly to five different SPAR units. The nutrient solution for each treatment was mixed using five separate irrigation tanks with an agitator at the bottom to ensure that each mixture stayed in the solution. Each solution was equally applied to an assigned experimental unit (pot) for 60 s three times per day throughout the experimental period, as in the previous experiments (Reddy and Matcha, 2010; Zhao et al., 2005; Zhao et al., 2003). The amount of the respective nutrient solution delivered was 120% of the estimated evapotranspiration of the previous day. The excess solution was drained through the hole in the bottom of each pot and the SPAR soil bins (Reddy et al., 2001).

2.4 Measurements

Measurements were destructively collected on six plants per treatment every seven days post-emergence (5 days after sowing, DAS) for four measurement events, hereafter termed harvest date.

2.4.1 Physiologic parameters

The leaf chlorophyll content (CHL, $\mu g \cdot cm^{-2}$), flavonoids (FLAV, unitless), anthocyanins (ANTH, unitless), and N balance index (NBI, unitless), the ratio between chlorophyll and flavonoids and a measure of leaf N, were measured on the recently expanded uppermost leaf with a developed collar using a hand-held Dualex leaf-clip sensor (DX16641, ForceA Scientific Instruments, Paris, France).

Net photosynthesis (Pn, $\mu mol \cdot m^{-2} \cdot s^{-1}$), stomatal conductance (Gs, $mmol \cdot m^{-2} \cdot s^{-1}$), and the internal-to-external CO_2 concentration ratio (Ci/Ca) were also measured on the uppermost leaf with a developed collar for each plant. These measurements were recorded between 10:00 and 12:00 h on each harvest day using a Li-6400XT portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA). The LED light source was set to 1500 $\mu mol\ m^{-2} \cdot s^{-1}$, the temperature inside the leaf chamber was 30°C, relative humidity was adjusted to ambient levels, and leaf chamber CO_2 was maintained at 420 $\mu L \cdot L^{-2}$.

2.4.2 Shoot growth and development

At each harvest time, plants were cut at the soil surface to separate the shoot from the root system. Plant height (PH, $cm \cdot plant^{-1}$) was manually measured using a standard metric ruler as the distance from the soil surface to the uppermost leaf collar. Next, leaf number (LN, no. $\cdot plant^{-1}$) was counted as the number of leaves with collars. Then, leaves were separated from the stem at the leaf collar and measured for leaf area (LA, $cm^2 \cdot plant^{-1}$) using an LI-3100 leaf area meter (LI-COR Inc.). All leaves actively developing above the uppermost collared leaf were cut at the location of the uppermost collar.

2.4.3 Root growth and development

Root systems and soil media were gently removed from the PVC pots and washed with a gentle stream of water over a wire mesh sieve to wash the sand and gravel away until the roots were clean. Next, individual root systems were floated in a 400 × 300 cm acrylic tray filled with 5 mm of water, and roots were carefully untangled using plastic forceps to minimize overlap and ensure quality imagery. The trays were placed on an Epson Expression 11000XL scanner (Epson America, Inc., Long Beach, CA, USA), and digital images were acquired at a resolution of 31.5 dot mm. These images were analyzed using WinRHIZO Pro 2009C software (Regent Instruments, Inc., Québec, Canada). The root analysis provided a quantified estimate of root growth and development parameters: root tips (RT, no.·plant^{-1}), root forks (RF, no.·plant^{-1}), total root length (TRL, cm·plant^{-1}), root surface area (RSA, cm^2·plant^{-1}), and root volume (RV, cm^3·plant^{-1}).

2.4.4 Dry matter accumulation

Finally, the separated leaves, stems, and roots were individually bagged and oven-dried on-site at 80°C for three days to ensure a constant weight was reached. These samples were quickly weighed for leaf dry weight (LDW, g·plant^{-1}), stem dry weight (StDW, g·plant^{-1}), and root dry weight (RDW, g·plant^{-1}). Total dry weight (TDW, g·plant^{-1}) was calculated as the sum of all three components per plant.

Leaf and stem dry matter material were combined for each plant, and tissue N concentration was measured in three dried ground samples using methods described previously (Nelson and Sommers, 1973). Nitrogen concentration was expressed as g·kg^{-1} shoot dry weight.

At the fourth harvest, the leaves, stems, and roots were also measured for N concentration to compare the relationship between shoot N concentration and the N concentration of the individual components.

2.5 Statistical Analysis

The experiment was designed as a split-plot, with N treatments as the main plot and harvest timing as the subplot. Each treatment consisted of 30 pots, and six pots were randomly selected for destructive measurement at each harvest. Shoot N concentration and all parameters were analyzed for treatment effects, harvest timing, and interaction using PROC ANOVA and Fisher's LSD. tests at $p = 0.05$ (SAS v. 9.4, SAS Institute, Cary, NC, USA). The Sigma Plot v.13 (SysStat Software Inc., San Jose, CA, USA) was employed to generate graphs and perform regression analysis.

Growth rates for each parameter were calculated depending on their growth pattern over time. Absolute growth rates were calculated for all parameters displaying linear growth over time:

$$AGRp = \frac{Wp1 - Wp2}{t2 - t1}, \tag{1}$$

where $AGRp$ is the absolute growth rate of parameter p, $Wp1$ is the mean value of parameter $p1$ at $t1$, $Wp2$ is the mean value of parameter $p2$ at $t2$, and $t1$ and $t2$ are the days of harvest after treatments were imposed.

Relative growth rates were calculated for all parameters displaying exponential growth over time. The mean relative growth rate was determined as described by Fisher (1921):

$$RGRp = \frac{\ln W2 - \ln W1}{t2 - t1}, \tag{2}$$

where $RGRp$ is the relative growth rate of parameter p, $W1$, and $W2$ are the measured values of parameter p at $t1$ and $t2$, and $t1$ and $t2$ are the time $W1$ and $W2$ were observed.

For parameters exhibiting a nonlinear relationship between growth rates and shoot N concentration, optimal N concentration was estimated as the vertex of the function. The vertex represents the N concentration where the parameter is occurring at its maximum, and any further increases in N are estimated to yield no additional increase.

3 Results

Plant nitrogen concentration

Plants were grown 5 to 33 days after sowing (DAS) and supplemented with nutrient solutions containing different N concentrations. These solutions resulted in different N concentrations of the shoot or above-ground plant parts. Shoot N concentration significantly differed depending on the treatment and harvest timing (Table 1). Treatment effects were observed quickly and were evident after just seven days of treatment. As the experimental period progressed, shoot N concentration declined under all treatments (Fig. 1). The average shoot N concentration was 39.2g·kg^{-1}, 32.5g·kg^{-1}, 24.0g·kg^{-1}, 20.2g·kg^{-1}, and 11.9 g·kg^{-1} for the 100%, 60%, 20%, 10%, and 0% N treatments, respectively.

Plants harvested 28 days after treatment (DAT) or 33 days after sowing (DAS) were independently analyzed for N concentration in the leaves, stems, and roots. The resulting N concentrations of the individual components were all linearly correlated to shoot N concentration. The relationships to shoot N concentration (%) were best fitted by the following functions:

$$\text{Leaf N\%} = 1.0343 \times (\text{Shoot N\%}), \quad R^2 = 0.98, \tag{3}$$

$$\text{Stem N\%} = 0.97 \times (\text{Shoot N\%}), \quad R^2 = 0.99, \tag{4}$$

$$\text{Root N\%} = 0.5839 \times (\text{Shoot N\%}), \quad R^2 = 0.98. \tag{5}$$

Photosynthesis

The N treatment and harvest timings significantly affected leaf photosynthesis rates (Fig. 2). As the treatment duration progressed, photosynthesis increased for the 100% and 60% N treatments but declined for the 20%, 10%, and 0% N treatments (Data not shown). The photosynthesis rate increased linearly as shoot N concentration increased (Fig. 2(a)). The highest photosynthesis rate (50.2 μmol·m^{-2}·s^{-1}) was observed at 28 DAT under the 100% N treatment when plants contained an average shoot N concentration of 29.1 g·kg^{-1}. Conversely, the lowest leaf photosynthesis rate

Table 1 Summary of analysis of variance across the harvest date (HD), nitrogen treatment (N), and their interaction (HD × N) on different root and shoot growth, physiological, and developmental traits measured weekly after emergence.

Source	**PH**	**LN**	**LA**	**LDW**	**StDW**	**RDW**	**TDW**	**L%**	**S%**
Harvest Date (HD)	***	***	***	***	***	***	***	***	***
N Level (N)	***	***	***	***	***	*	***	***	***
HD×N	***	***	***	***	***	NS.	***	***	***
Source	**R%**	**RS**	**TRL**	**RSA**	**RV**	**RT**	**RF**	**N %**	
Harvest Date (HD)	***	***	***	***	***	***	***	***	
N Level (N)	***	***	***	***	***	***	***	***	
HD×N	*	**	***	***	***	NS.	***	***	

Notes: *, **, *** represent significance levels at $p \leqslant 0.05$, $p \leqslant 0.01$, and $p \leqslant 0.001$, respectively. NS represents non-significant. Values are the mean of six replications for each harvest date at each temperature treatment. Plant height (PH), leaf number (LN), leaf area (LA), leaf dry weight (LDW), stem dry weight (StDW), root dry weight (RDW), total dry weight (TDW), root-to-shoot ratio (RS), total root length (TRL), root surface area (RSA), root volume (RV), root tips (RT), root forks (RF); and leaf (L%), stem (S%), and root (R%) dry weight as a fraction of total dry weight. Shoot N concentration of leaf and stem dry matter (N%).

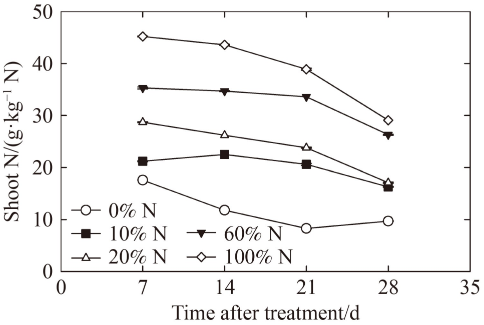

Fig. 1 Corn shoot N concentration over time for each treatment. Shoot N concentration differed significantly among the treatments ($p \leqslant 0.05$) and declined over time for all treatment levels. The error bars are shown if the values are larger than the symbol size.

(10.2 μmol·m^{-2}·s^{-1}) was observed at 28 DAT under the 0% N treatment when plants contained an average shoot N concentration of 9.7 g·kg^{-1}, and 80% decline compared to that observed under the 100% N treatment at the same harvest time.

Stomatal conductance was affected by the N treatment and duration, and the response trend was like photosynthesis (Fig. 2(b)). Generally, stomatal conductance increased quadratically as shoot N concentration increased. The highest and lowest stomatal conductance were observed 28 DAT under the 100 and 0% N treatment.

The internal-to-external CO_2 concentration ratio (Ci/Ca) was negatively correlated with increasing shoot N concentration (Fig. 2(c)). Thus, despite low leaf photosynthesis rates corresponding with low stomatal conductance under decreased shoot N concentration, the internal CO_2 concentration was highest under reduced N concentration and declined as shoot N concentration increased.

Leaf pigments

Changes over time in chlorophyll and the NBI in the uppermost collared leaf were like those observed for photosynthesis (Fig. 3). Over time, an increase was

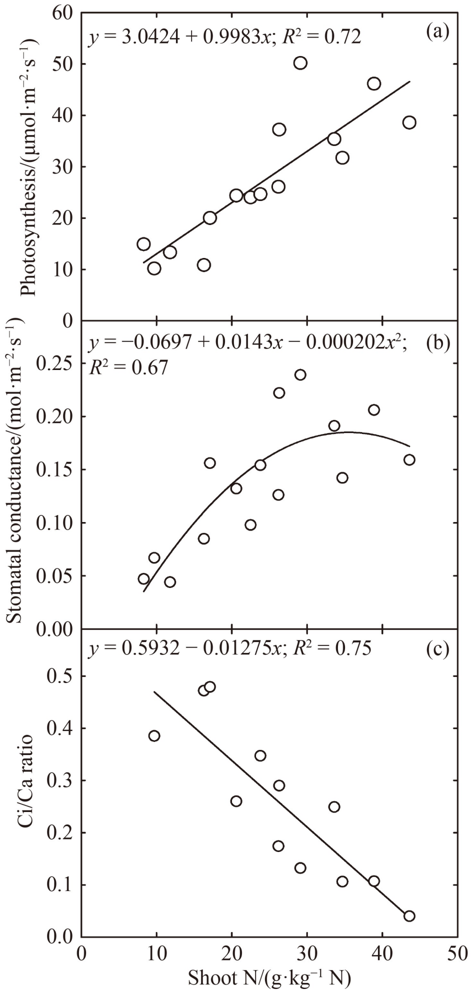

Fig. 2 Functional relationships between corn shoot nitrogen (N) concentration and (a) photosynthesis, (b) stomatal conductance, and (c) internal-to-external carbon dioxide (CO_2) concentration ratios (Ci/Ca) during the supplemental N treatments. Photosynthesis (a) and internal-to-external carbon dioxide concentration ratios (c) fit a linear function. Stomatal conductance (b) best fits a quadratic function. All values are the mean of six replications at each harvest under each treatment. All three functions are significant at the $P = 0.05$ level.

observed for the 100% and 60% N treatments, but values declined for the 20%, 10%, and 0% N treatments. Chlorophyll concentration was positively correlated to shoot N concentration (Fig. 3(a)). The relationship was the best fit by a quadratic equation with an estimated optimal N concentration of 41.3 $g \cdot kg^{-1}$. The highest chlorophyll concentration of 40.56 $\mu g \cdot cm^{-2}$ was observed at 28 DAT under the 100% N treatment. The lowest chlorophyll concentration of 3.34 $\mu g \cdot cm^{-2}$ was observed at 28 DAT under the 0% N treatment, a 92% decrease from that observed under the 100% N treatment. The NBI exhibited a similar positive relationship with shoot N concentration, increasing quadratically as the shoot N concentration increased, with an estimated optimal shoot N concentration of 40.8 $g \cdot kg^{-1}$. The NBI displayed maximum and minimum values at the same treatment combinations observed for chlorophyll concentration (Fig. 3(b)).

Flavonoids and anthocyanins reached their highest levels under very low N concentrations, with the highest values observed under the 0% N treatment at all four harvests. Flavonoids and anthocyanins declined quadratically as the shoot N concentration increased. The trend for anthocyanins was essentially the inverse of that observed for chlorophyll and the NBI; the highest anthocyanin value of 0.332 was observed at 28 DAT under the 0% N treatment, whereas the lowest anthocyanin value of 0.094 was observed at 28 DAT under the 100% N treatment, representing a total anthocyanin reduction of 73% (Fig. 3(d)).

Shoot morphology

As plants grew from 5 to 33 DAS (0 to 28 DAT), plant height and the number of collared leaves per plant increased linearly, but these increases depended upon treatment (Figs. 4 and 5, Table 1). At the final harvest (28 DAT), the tallest plants were observed under the 100% N treatment (Fig. 5 (a)). Final plant height declined by 39.6, 60.5, 72.9, and 84.5% for plants under the 60%, 20%, 10%, and 0% N treatments, respectively (Fig. 5(a)). Plants under the 100% and 60% N treatments developed the highest number of leaves per plant, whereas plants subjected to the 0% N treatment produced the lowest number of leaves per plant (Fig. 5(b)). Plant height and leaf number increased linearly over time; thus, stem extension rate and leaf addition rate were best calculated as the absolute growth rate of these two parameters. The relationship between stem extension rate and shoot N concentration fits a concave quadratic function (Fig. 5 (d)). As shoot N concentration declined from 39.2 $g \cdot kg^{-1}$ to 32.4 $g \cdot kg^{-1}$, the stem extension rate declined by 25%. On the other hand, the leaf addition rate was best fit into a linear relationship with shoot N concentration (Fig. 5 (e)).

The whole plant corn leaf areas were 663 $cm^2 \cdot plant^{-1}$, 401 $cm^2 \cdot plant^{-1}$, 257 $cm^2 \cdot plant^{-1}$, 166 $cm^2 \cdot plant^{-1}$, and

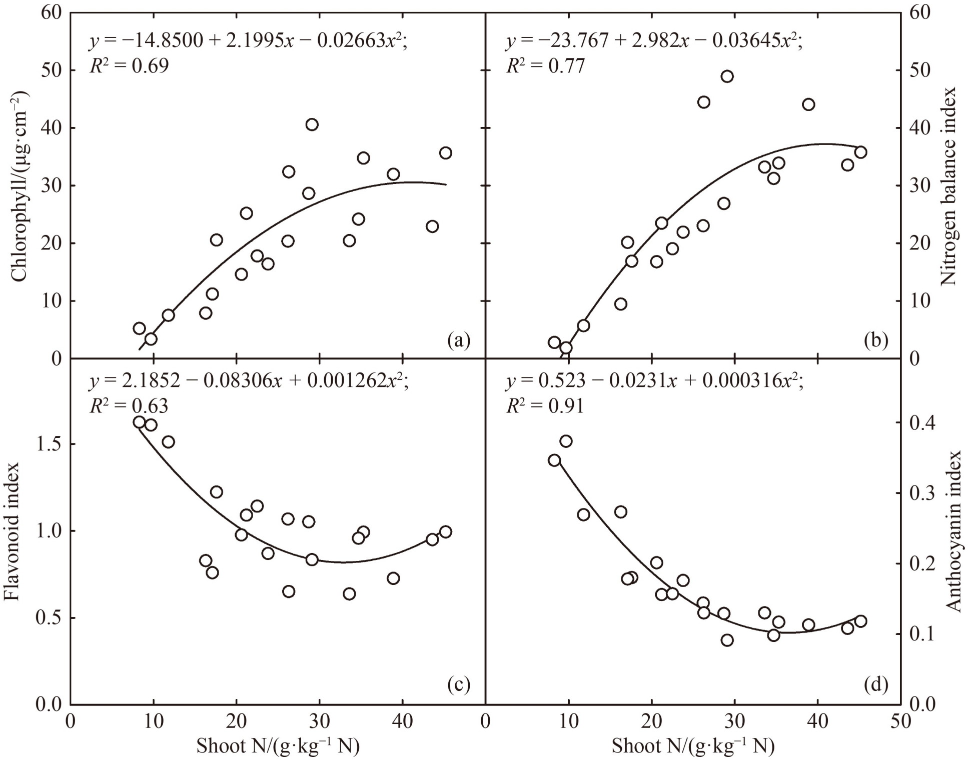

Fig. 3 Functional relationships between corn shoot N concentration and (a) leaf chlorophyll concentration, (b) nitrogen balance index, (c) flavonoid index, and (d) anthocyanin index during the supplemental N treatments. The chlorophyll concentration (a), nitrogen balance index (b), flavonoid index (c), and anthocyanin index (d) were all fit to a quadratic function. All values are the mean of six replications at each harvest under each treatment.

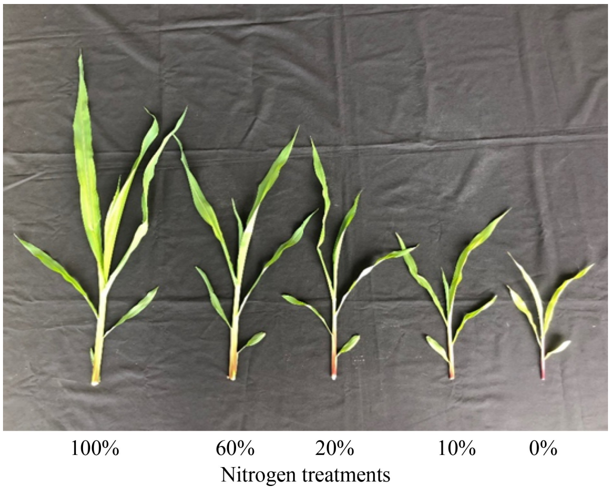

Fig. 4 Pictorial representation of corn shoot growth under five N treatments, harvested 14 days after treatment and 20 days after sowing.

87 $\text{cm}^2 \cdot \text{plant}^{-1}$ under control 100%, 60%, 20%, 10%, and 0% nitrogen treatments, respectively. Similarly, other parameters varied among the N treatments (Fig. 5). Leaf area per plant increased exponentially as the experimental period progressed and differed among the N treatments at each harvest (Table 1, Figs. 4 and 5(c)). Plants grown under the 100% N treatment consistently achieved the greatest leaf area across all four harvests. The leaf area expansion rate was calculated as the relative growth rate of leaf area per plant over time. The leaf area expansion rate increased linearly as shoot N concentration increased (Fig. 5(f)). As shoot N concentration declined from 39.2 $\text{g} \cdot \text{kg}^{-1}$ to 32.4 $\text{g} \cdot \text{kg}^{-1}$ N, the relative leaf area expansion rate decreased by 29.5%. The lowest leaf area expansion rate of 0.0645 $\text{cm}^2\ \text{cm}^{-2}$ was observed for plants grown under the 0% N treatment with an average shoot N concentration of 11.9 $\text{g} \cdot \text{kg}^{-1}$ N, representing a decline of 66% compared to that of the control.

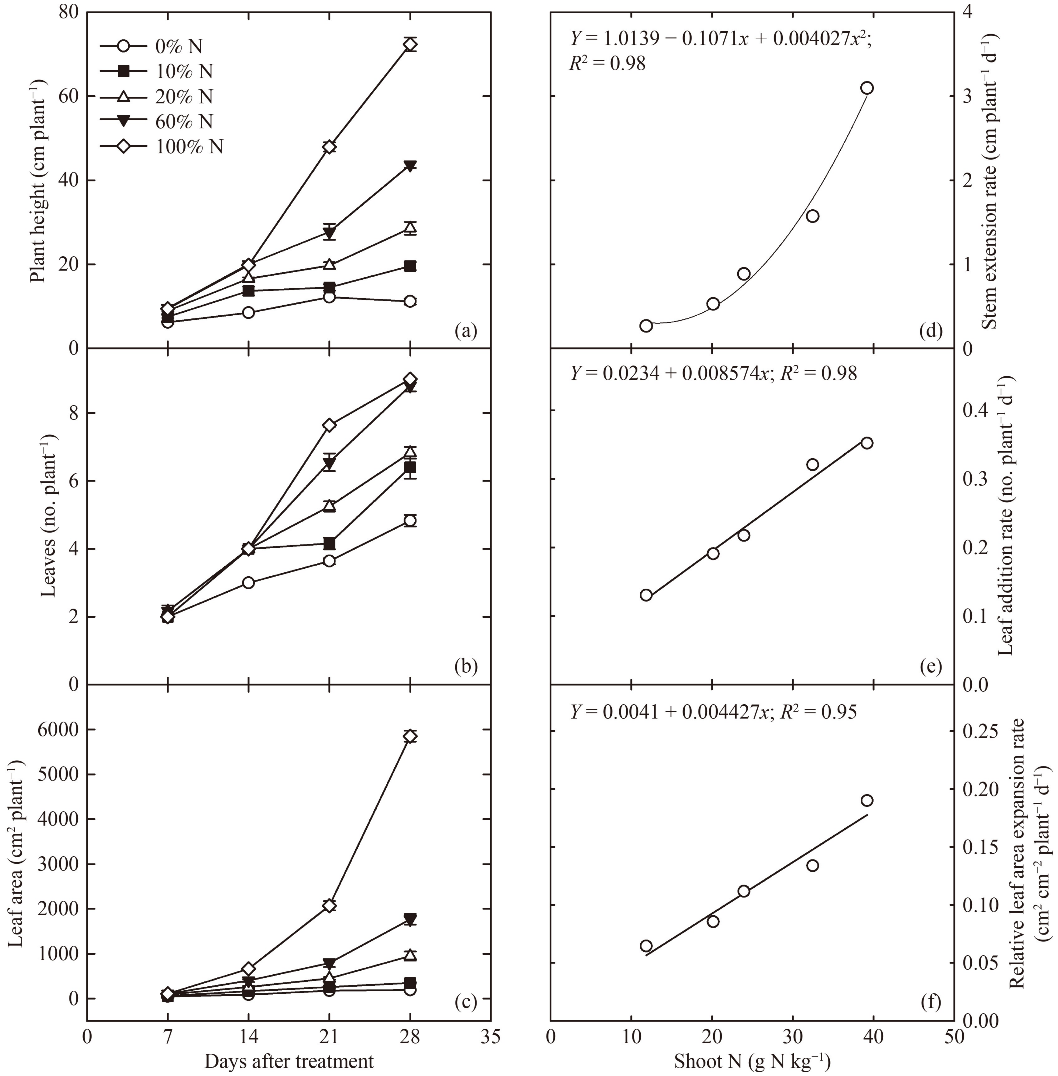

Fig. 5 Temporal trends in corn (a) plant height, (b) leaf number, and (c) leaf area during the four supplemental N treatment harvests. Rates of (d) stem extension, (e) leaf addition, and (f) leaf area expansion are expressed as a function of shoot N concentration. All values are the mean ± standard error of six replications at each harvest under each treatment. Stem elongation (d) was the best fit for a quadratic function: leaf addition rate (e) and leaf area expansion rate (f) best fit linear functions.

Fig. 6 Pictorial representation of corn root growth and development under five N treatments, harvested 14 days after treatment and 20 days after sowing.

Root morphology

All root growth and development parameters exhibited similar trends throughout the experimental period and primarily showed exponential growth patterns. The lowest root growth and development was observed at all four harvests in plants subjected to the 0% N treatment (Figs. 6, 7, and 8). At the final harvest (28 DAT), total root length and root surface area did not differ among the 100%, 60%, and 20% N treatments. However, root volume under the 100% N treatment was significantly higher than all other N treatments at the final harvest. Root development displayed similar trends. Plants grown under the 100% and 60% N treatments produced the greatest number of root tips at the final harvest (Fig. 8). Root fork development did not differ among the 100%, 60%, and 20% N treatments at 28 DAT. Relative growth rates were calculated for all root growth and development parameters, and all these rates held a quadratic relationship with shoot N concentration (Figs. 7 and 8). As shoot N concentration declined, the decrease in relative growth rates of all root parameters became more pronounced. The optimal shoot N concentration for maximal relative growth of all root traits was estimated as the apex of the fitted quadratic function. These computations yielded 36.9 $g \cdot kg^{-1}$ N for total root length, 38 $g \cdot kg^{-1}$ N for root surface area, 41.2 $g \cdot kg^{-1}$ N for root volume, 42.8 $g \cdot$ N kg^{-1} for root tips, and 42.7 $g \cdot kg^{-1}$ N for root forks.

Plant component dry weights

The dry weight of leaves, stems, and roots followed exponential growth trends as the experimental period progressed. Leaf and stem dry weights at all harvests were highest under the 100% N treatment and the lowest under the 0% N treatment (Fig. 9). At the final harvest (28 DAT), the highest root dry weight was produced under the 100% N treatment. At the 7 and 14 DAT harvests, a moderate reduction in the supplemental N concentration in the nutrient solutions stimulated dry weight accumulation in the roots, with the highest root dry weight observed at 7 and 14 DAT under the 60% N treatment. Relative growth rates for leaves, stems, and roots were fitted as a function of average shoot N concentration. The relative leaf dry weight accumulation is positive and linearly fit to shoot N concentration. Stem and root-relative dry weight accumulation best-fit convex quadratic functions in relation to shoot N concentration, with a greater rate of decline at low shoot N concentrations. Moderate reduction of N in nutrient solution limited leaf dry weight more than stem and root dry weight accumulation. For example, a decline in average shoot N concentration from 39.2$g \cdot kg^{-1}$ to 32.5 $g \cdot kg$ N^{-1} resulted in a 25.3%, 19.4%, and 12.5% decline in relative leaf, stem, and root dry weight accumulation. However, these trends differed as N became extremely limited in solution. Plants grown under the 0% N solution with an average shoot N concentration of 11.9 $g \cdot kg^{-1}$ N displayed a 68.8%, 63.8%, and 70.8% decline in relative dry weight accumulation in leaf, stem, and root (Fig. 9).

4 Discussion

A thorough literature search reveals that only a few reports evaluated N concentrations during late vegetative growth stages around V14–15 (Ciampitti and Vyn, 2011; Ciampitti et al., 2013). Alternatively, studies investigating the efficacy of optical canopy sensing tools for improving N management at early vegetative stages found poor predictability of corn grain yield at early corn growth stages before V6 (Tagarakis and Ketterings, 2017; Paiao et al., 2020). Moreover, Colaço et al. (2021) questioned the use of simplistic variables by existing sensor-based N management strategies and recommended the use of information from multiple variables. Our research is one of the first attempts to provide functional algorithms at early corn growth stages. Incorporating the relationship established between N and early plant morphophysiological will improve N rate recommendation for late split applications. Also, this is the first study to provide functional algorithms for plant processes, including root

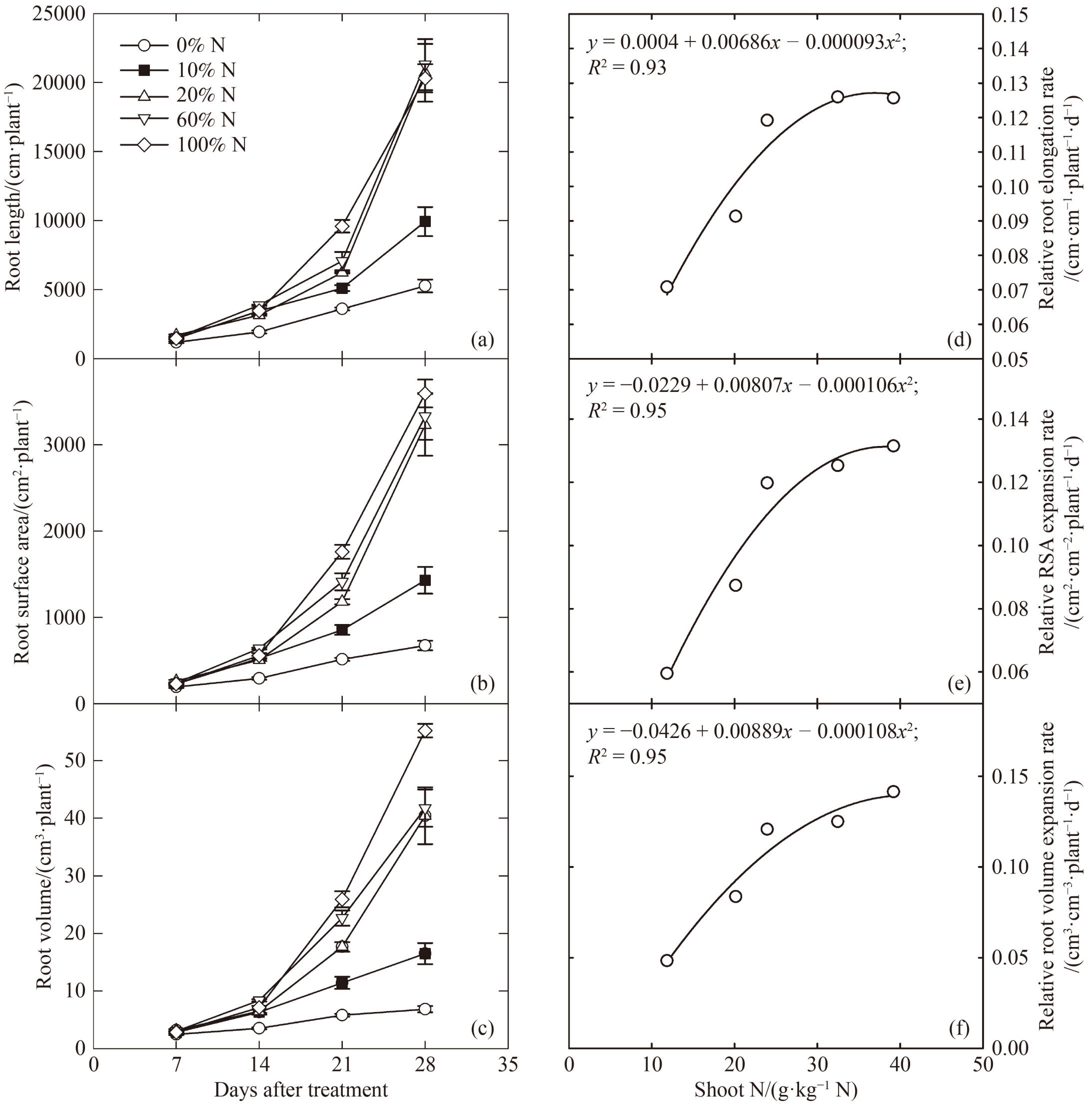

Fig. 7 Temporal trends in corn root growth of (a) root length, (b) root surface area, and (c) root volume during the four N treatment harvests. Relative growth rates of (d) root elongation, (e) root surface area expansion (RSA), and (f) root volume expansion as a function of measured shoot N concentrations. Expansion rates for root elongation, root surface area, and root volume best fit quadratic functions. All values are the mean ± standard error of six replications at each harvest under each treatment.

growth and development, that could improve the functionality of the corn models for field applications. Shoot N concentration decreased over time for all N treatments, including the control showing the interplay between corn growth and nutrient acquisition. Previous research suggests this illustrates critical N concentration's dynamic and ontogenetic characteristics in plants. The critical N concentration is a plant's minimum N concentration to produce maximal aerial biomass at a given developmental stage (Plénet and Lemaire, 1999). For plants that uptake adequate N, the critical N concentration is expected to decline over time due to optimal biomass production and N allocation to structural and storage materials containing lower N concentrations than photosynthetic materials (Broadley et al., 2000). Plénet and Lemaire (1999) also suggested that leaf self-shading can induce the non-uniform distribution of N within plants and even within individual leaves.

Plants depend on internal N sources to maintain maximal growth when N availability in soil is limited. Leaves in the higher canopy that receive higher solar radiation levels are expected to contain higher N concentrations than leaves in the lower canopy, which are often shaded. Even under limiting N supplies, plants can translocate N from older, lower canopy leaves to actively growing meristematic regions in the higher canopy, where younger leaves develop, expand, and receive higher solar radiation levels. This N translocation to the upper canopy can be technically problematic for studies estimating plant N concentrations at the canopy level using remote sensing technology (Raper et al., 2013). Our study established that photosynthesis, chlorophyll concentration, and the NBI in the uppermost collared leaf correlated with shoot N concentration. However, there

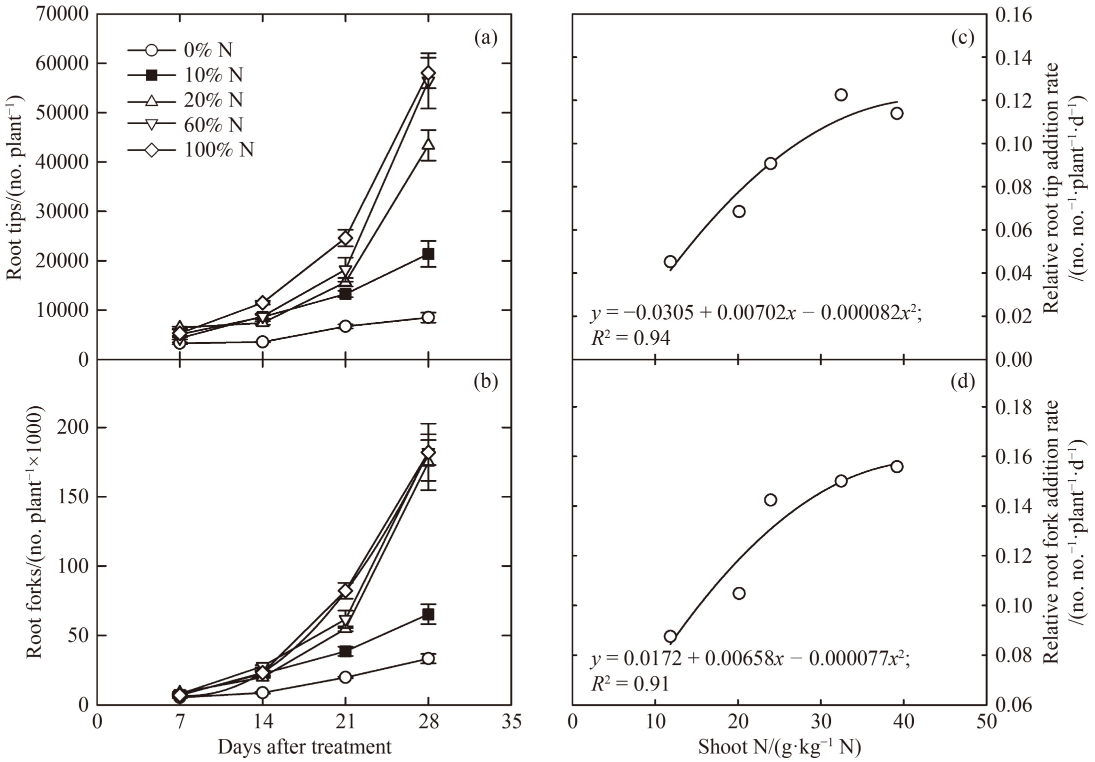

Fig. 8 Temporal trends in corn root development as measured through (a) root tips and (b) root forks during the four supplemental N treatment harvests. Relative root developmental rates of (d) root tips and (e) root forks as a function of measured shoot N concentrations. All values are the mean ± standard error of six replications at each harvest under each treatment. Root tip and root fork addition rates were fit to a quadratic function.

were stronger correlations between photosynthesis and the chlorophyll concentration or photosynthesis and NBI (Fig. 10). The chlorophyll concentration and NBI may better reflect the N status of the measured leaf than the entire shoot. Thus, the results of this study support the proposal that leaf-level photosynthesis is closely related to the local N concentration in the leaf. That leaf N concentration varies within a plant under adequate and limiting shoot N concentrations. Also, the decline in photosynthesis was more related to non-stomatal limitation as Ci/Ca values were more significant under N stress conditions, as observed in other studies (Reddy and Matcha, 2010; Reddy et al., 1997). Ciompi et al. (1996) reported similar results; under N stress in leaves, reduced photosynthesis and increased stomatal conductance were accompanied by increased intercellular CO_2 concentration. Similarly, they suggested that the reduction in photosynthesis was due to reduced mesophyllic activity rather than stomatal activity. However, a recent review by Collmenero-Flores et al. (2019) points out that optimal growth of plants requires a synchronous supply of Cl^{-1} and NO_3^- molecules. They also pointed out that plant selectivity varies between species and varieties, and environmental conditions modify some. In our study, we did not measure shoot chloride content, and therefore, it is not easy to ascertain the relative roles of Cl^{-1} and NO_3^- in the gas exchange process.

Plant growth rate represents the ability of a plant to capture resources and convert those resources into biomass (Peng et al., 2010). Ågren (1985) suggests a simple linear relationship between plant N concentration and relative growth rate. Our results are consistent with this hypothesis. As shoot N concentration declined below 39.2 g·kg^{-1} N, there was a linear decrease in the relative growth rate (defined as biomass produced per unit biomass) (Fig. 11). The physiologic component of the relative growth rate is called the leaf assimilation rate, which is an expression of the relative increase in biomass per unit of leaf area (Broadley et al., 2000). In our study, a quadratic function best described the leaf assimilation rate with an estimated optimal N concentration of 31.7 g·kg^{-1} N. This value represents the total assimilates produced by photosynthesis minus those lost to respiration per unit leaf area. These results indicate that the increase in biomass per unit leaf area is less sensitive to N stress than the relative increase per unit biomass.

Two major factors could cause this outcome. First, plants can mobilize enough N to maximize photosynthesis in leaves under moderate N stress, intercepting the most solar radiation. Second, plants are subject to the "functional equilibrium concept". Brouwer (1962) initially proposed this concept, assuming that the supply of carbon limits root growth from leaf

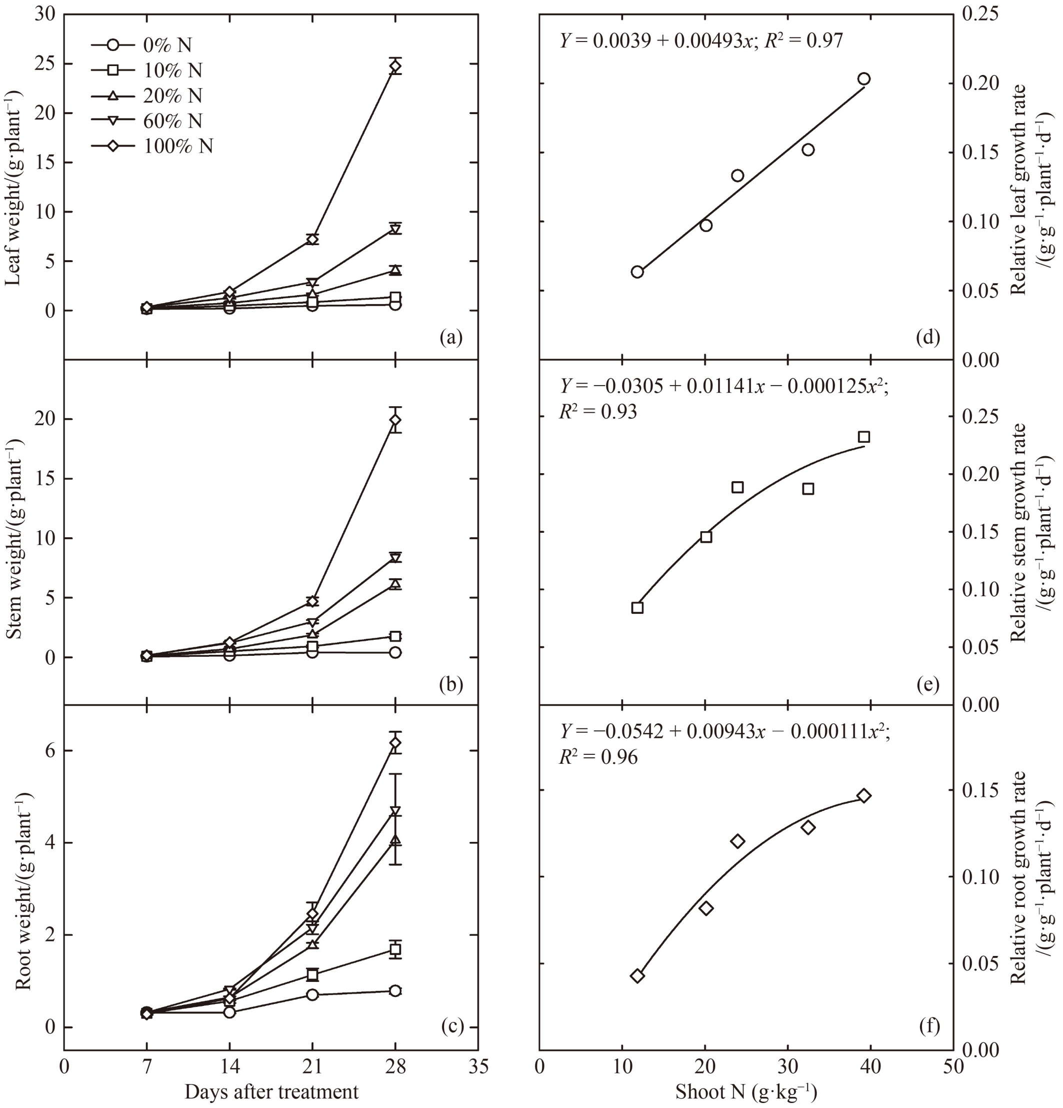

Fig. 9 Dry weight accumulation for corn (a) leaves, (b) stems, and (c) roots during the experimental period. Relative root growth rates of corn (d) leaves, (e) stems, and (f) roots during the experimental period were expressed as a function of measured shoot N concentrations. All values are the mean ± standard error of six replications at each harvest under each treatment. Relative leaf growth rate (d) best fits a linear function. The relative stem (e) and root (f) growth rates best fit quadratic functions.

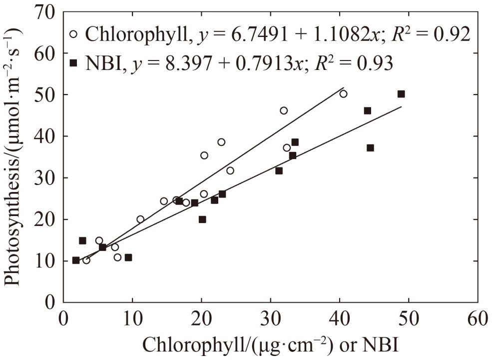

Fig. 10 Functional relationships between corn-measured chlorophyll concentration or nitrogen balance index (NBI) during and photosynthesis during the supplemental N treatment period. All values are the mean of six replications at each harvest under each treatment. Photosynthesis rates were best fit for a linear function of chlorophyll concentration or nitrogen balance index values.

photosynthesis and that leaf growth is limited by water and nutrients from the root system. Kruse et al. (2010) also suggest that plants adjust their resource allocation to optimize their architecture and resource allocation to address limiting factors and maintain the highest possible growth rate. Thus, as N concentration moderately declined, plants may prioritize carbon resources to the root system to increase the uptake capacity of the limiting resource, N, in this case. This altered carbon allocation does not maximize the return on investment in carbon production if the carbon resource was invested in photosynthetically active structures. Still, it does allow the plant to attempt to maintain functional equilibrium and acquire the needed resources to sustain future optimal growth. In our experiment, the observed increase in the root-to-shoot ratio as shoot N concentration declined further supports this hypothesis. As shoot N concentration

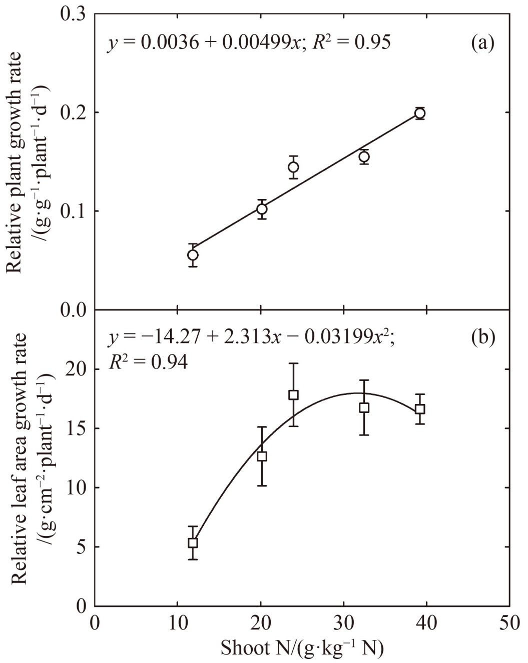

Fig. 11 Functional relationships between corn shoot N concentrations and (a) whole-plant relative growth rate and (b) whole-plant relative leaf growth during the supplemental N treatment period. All values are the mean ± standard error for all replications across all four harvests under each treatment. The relative plant growth was best fit a linear function, and the relative leaf area expansion rate was best fit to a quadratic function to shoot N concentration.

decreased, sufficient N was unavailable to maximize the allocation of carbon resources to build photosynthetic structures; thus, the plant allocated more carbon to the root system to acquire the needed N.

In our study, plants allocated a more significant portion of their biomass to the root system as N concentration declined and became more limiting, likely to uptake more N, which reduced biomass investment in photosynthetically active structures (Fig. 12). Thus, plants maintained biomass per unit leaf area under limiting N but invested in systems that increased their ability to capture more N than structures that created more biomass or leaf area.

During the first two harvests, the most significant root systems were produced by plants subjected to the 60% N nutrient solution and thus were experiencing moderate N stress. However, as N stress became too limiting and reduced the photosynthetic capacity of the plant canopy, C also became a limiting factor for root growth. Despite an increased root shoot ratio, a minor overall root system was observed at the third and fourth harvests. The results of this study are further supported by Peng et al. (2010), who reported that corn root growth is coordinated with shoot growth and shoot nutrient demands. Thus, plant root formation keeps pace with plant shoot development and demands nutrients and moisture.

Plants have multiple mechanisms to maximize nutrient acquisition, such as developing a more extensive root system, altering the root architecture, or increasing the transmembrane nutrient uptake rate. In our study, although plants allocated more biomass to the root system as shoot N concentration declined, the proportion of different root structures per unit of root biomass remained unchanged. All root morphological parameters were significantly and positively correlated to root biomass across all experimental treatments and durations (Fig. 13, Table 2), including total root length (R^2 = 0.93), root surface area (R^2 = 0.97), root volume (R^2 = 0.99), root tips (R^2 = 0.97), and root forks (R^2 = 0.93). These results suggest that crop modeling can be optimized by focusing on biomass allocation to estimate plant root systems' status and resource uptake potential under N stress. Similarly, breeding programs may be optimized by selecting plants with the greatest root biomass and optimized root-to-shoot ratios to develop plants with the greatest ability to explore the surrounding soil environment for resource-limiting nutrients.

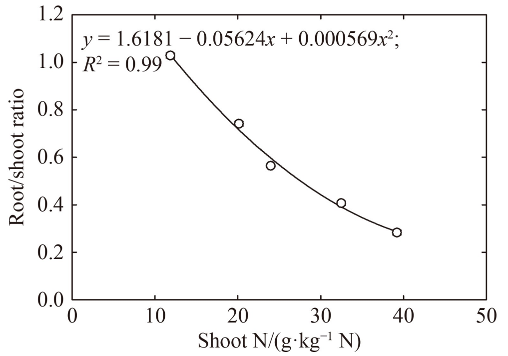

Fig. 12 Functional relationships between corn root and shoot ratios and measured shoot N concentrations during the supplemental N treatment period. All values are the mean of six replications across all four harvests under each treatment. A quadratic function best describes the relationship between root-to-shoot ratio and shoot N concentration.

The potential root and shoot growth, developmental parameters, and physiologic traits under optimum temperature conditions, and the respective growth rate response indices under a broad range of nutrient conditions should help develop new subroutines or improve corn simulation models (Jones and Kiniry, 1986; Lizaso et al., 2003; Yang et al., 2009) for field applications and in policy areas (Jägermeyr et al., 2020; Reddy et al., 1997; Reddy et al., 2008). In addition, the influence of other environmental stress factors, such as ultraviolet-B radiation (Reddy et al., 2013), soil waterlogging (Walne and Reddy, 2021), temperature (Walne and Reddy, 2022), nutrients (Zhao et al., 2003), and water stress (Wijewardana et al., 2017) on corn growth and developmental processes are required to decrease the potential corn growth and simulate the performance under field condition. Future research should also address reproductive yield and grain quality as a function of N under optimum water and nutrient conditions.

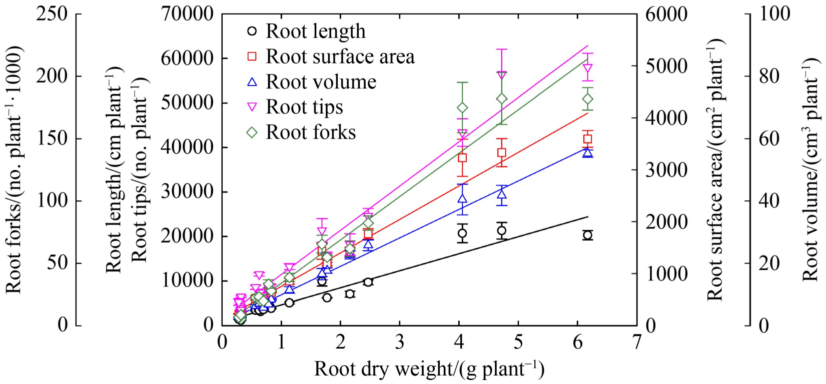

Fig. 13 Functional relationships between corn root weight, root growth, and developmental parameters during the supplemental N treatment period. All root growth parameters showed a linear relation with corn root weights. All values are the mean ± standard error of six replications at each harvest under each treatment.

Table 2 Regression parameters (*a* and *b*) and coefficient of determination (R^2) of corn root growth and developmental parameters as a function of root weight measured during the early season

Parameters	Regression coefficients		R^2
	a	*b*	
Root length, cm·plant^{-1}	847.87	3823.33	0.93
Root surface area, cm^2 ·plant^{-1}	0.7135	9.1397	0.99
Root volume, cm^3 plant^{-1}	108.42	645.18	0.97
Root tips, no. plant^{-1}	1504.16	9944.53	0.97
Root forks, no. plant^{-1}	−922.19	34806.98	0.95

5 Conclusions

Corn physiological, growth, and developmental traits, including major root traits, responded with changes in shoot N levels. The decline in photosynthesis was primarily due to non-stomatal limitation than the decline in stomatal conductance with declining shoot N levels and Ci/Ca negatively correlated with declining shoot N. Plants under stressed conditions downregulated physiology, including gas exchange parameters and chlorophyll concentration and N balance indices and upregulated protective mechanisms such as flavonoids and anthocyanins. Thus, shoot-N deficiency decreased leaf area and photosynthesis of corn plants, resulting in lower biomass. Even though all plant components declined with declining shoot N, the root-to-shoot ratio increased, allowing the plants to favor root growth and partitioning more biomass to root than shoot growth, enabling the plants to explore more nutrients under a given niche environment. The functional relationships between shoot N and growth and developmental processes, including roots, might be helpful to derive N-dependent environmental productivity indices as described by Reddy et al. (2008) to develop N-dependent models for N assessment and management of corn plants that are typically encountered under the field.

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