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Alterations in plant architecture and physiology allow maize to sustain yield after early defoliation

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Abstract

Maize (*Zea mays* L.) tolerance to early defoliation is shaped by genotype-specific physiological and morphological responses. Defoliation disrupts the source–sink balance, altering carbon allocation and plant development. Understanding these responses is crucial for optimizing breeding programs and agronomic management. In this study, the effects of complete canopy defoliation at vegetative stage 4 on growth parameters, root morphology, chlorophyll fluorescence, and yield stability in four maize genotypes were evaluated. Defoliation significantly reduced total leaf area, plant height, and root biomass while increasing root tissue density and the harvest index across all genotypes. Despite these structural changes, no significant differences were observed in key yield components, especially grain yield. Chlorophyll fluorescence analysis revealed distinct genotype-specific responses. Under defoliation, KWS9606 VIP3 exhibited enhanced photochemical efficiency at 9 days after defoliation (DAD) and increased quenching photochemical (qP) at 17 and 24 DAD. While BRS1010, qP increased under defoliation at all dates, suggesting greater openness of PSII reaction centers. NPQ responses were variable and lacked a consistent pattern, indicating diverse energy dissipation strategies. NS90 PRO2 exhibited

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Abbreviations: ANOVA, analysis of variance; DAD, days after defoliation; DAS, days after sowing; EMMs, estimated marginal means; HI, harvest index; LA, leaf area; NPQ, nonphotochemical quenching; PC1, first principal component; PC2, second principal component; PCA, principal component analysis; RF, root fineness; RMD, root mass density; RTD, root tissue density; SRL, specific root length; V4, vegetative stage 4.

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no significant differences between genotype × defoliation level combinations, reflecting limited physiological response. Principal component analysis highlighted the trade-offs between morphological and physiological adaptations, with root traits dominating first principal component and chlorophyll fluorescence parameters influencing second principal component. These findings indicate that maize genotypes exhibit diverse acclimation mechanisms to mitigate defoliation stress while maintaining yield stability. Understanding genotype-specific responses supports breeding programs aimed at improving tolerance to foliar loss and informs more resilient crop management strategies.

Plain Language Summary

Maize is among the most important cereal crops worldwide, and understanding how it responds to stress is crucial for improving agricultural practices. One such stress is defoliation—the loss of leaves due to natural events, such as wind or pests, or from mechanical actions, such as machinery traffic. In some modern farming systems, early defoliation is intentionally applied to improve planting schedules or resource use. Our research investigated how different maize genotypes respond to early defoliation by analyzing plant growth, root development, and physiological responses such as photosynthesis. We found that certain genotypes recover well from early leaf loss, maintaining productivity. These results highlight the potential to use defoliation strategically without harming yields. Our findings support more informed decisions in crop management and breeding, helping ensure resilient agricultural systems facing both planned and unexpected stresses.

1 | INTRODUCTION

Maize (*Zea mays* L.) is among the most important cereal crops worldwide and serves as a cornerstone of global food security. Brazil is the third-largest maize producer, with its production playing a critical role in both domestic and international markets (United States Department of Agriculture, Foreign Agricultural Service, 2024). As a C4 species, maize displays high adaptability to diverse environments because of its efficient photosynthetic pathway, which contributes to its importance in human nutrition, livestock feed, and various industrial applications (Prasanna et al., 2021). However, despite its physiological advantages, the long process of domestication has reduced the crop's genetic diversity and increased its susceptibility to environmental stresses. As a result, maize productivity increasingly faces threats from climate change, pest outbreaks, and agronomic challenges, many of which can lead to defoliation (Cairns & Prasanna, 2018; Guo et al., 2020).

Defoliation, characterized by the partial or complete removal of leaves, can significantly impact plant growth and yield, depending on its timing and severity. Early defoliation often results in little to no yield reduction, whereas late-season defoliation, which occurs closer to reproductive stages, can severely compromise grain production (Blanco et al., 2022, 2023). Similarly, partial defoliation may allow for recovery through compensatory growth, whereas complete defoliation typically leads to substantial biomass and yield losses (Blanco et al., 2023; Iqbal et al., 2012).

While often associated with crop stress, defoliation can also be integrated as a crop management tool. In Brazil, the Antecipe system exemplifies how early defoliation can be integrated into modern cultivation practices. This technique involves the mechanical sowing of maize between soybean rows, enabling earlier establishment of the second crop and reducing climate-related risks associated with delayed planting. In this system, defoliation of maize plants at the V3–V4 (vegetative stage 4) stage occurs mechanically during soybean harvest, when the combine cuts the canopy approximately 5 cm above the soil surface. Antecipe promotes the earlier establishment of the second crop, optimizing land use efficiency without compromising yield or grain quality (Karam et al., 2020). By advancing the maize cycle, this system leverages early-season growing conditions and has been increasingly adopted in regions aiming to intensify production sustainably.

Understanding plant responses to defoliation is thus directly relevant for validating and optimizing systems, such as Antecipe. Prior research suggests that maize can exhibit varying yield responses under defoliation stress, reflecting differences in their physiological and morphological adaptations. (Blanco et al., 2023; Zhang et al., 2024; Zheng et al., 2021). Studies by Jahan et al. (2022) and Y. Liu et al. (2023) further investigated the effects of defoliation on maize, yet the variability in genotype responses remains poorly understood. Understanding genotype-specific responses to defoliation is crucial for refining management practices within systems such as Antecipe and for guiding breeding program, enabling the identification and recommendation of genotypes that maintain yield stability under early leaf loss.

Therefore, the present study aims to explore the performance of different maize genotypes under early-stage defoliation in a context that mimics key aspects of the Antecipe system. To address these gaps, the morphological, physiological, and yield responses of four maize genotypes to defoliation were evaluated. By integrating growth parameters with chlorophyll fluorescence analyses, this study seeks to identify key traits contributing to genotype tolerance under conditions of leaf loss. Differences in sustaining energy production and optimizing resource partitioning likely contribute to genotypic variation in tolerance to defoliation.

Core Ideas

- We aimed to understand hybrid responses to early defoliation.
- We explored root and shoot traits under stress conditions.
- Genotypes showed distinct physiological adjustment strategies.
- The results support genotype selection and adaptive crop management.

2 | MATERIALS AND METHODS

The experiment was conducted in a greenhouse at the Santa Clara Educational Unit, part of the Federal University of Alfenas (UNIFAL-MG), located in the city of Alfenas, Minas Gerais, Brazil (altitude of 818 m above sea level; geographical coordinates: 21°25′20″ S latitude and 45°59′00″ W longitude). The mean maximum temperature was 35°C, the mean minimum temperature was 18°C, and the mean humidity was 79%.

Seeds were sown in 20-L pots filled with soil collected from the Santa Clara Educational Unit, which was taken from the top 20 cm of the soil surface. The soil type was classified as a typical Dystrophic Latosol (Oxisol). Nutrient levels were adjusted according to the guidelines established by Alvarez and Ribeiro (1999). The soil pH was corrected from 5.5 to pH 6 (±0.5) by lime application. Macronutrients were supplied using monoammonium phosphate (MAP) and potassium chloride, with the latter applied in fractions before planting and again 30 days after planting. Nitrogen was applied using two sources: MAP at planting and urea applied in three equal top-dress applications of 0.88 g each spaced 10 days apart following plant emergence. For micronutrient supplementation, boric acid, zinc sulfate, and manganese chloride were used (Table S1). Four seeds were placed in each pot, and after the seedlings emerged, two plants were maintained per pot. All the plants were watered daily until the soil approached field capacity. Phytosanitary control was performed with formulation containing the active ingredients thiamethoxam and lambda-cyhalothrin applied 45 days after sowing (DAS).

Each experimental unit consisted of a 20-L pot containing two maize plants. For statistical purposes, each pot was considered one replicate, totaling five replicates per factor combination. Four maize genotypes were evaluated, including two older single-cross hybrids (BRS1010 and BRS1055) and two modern commercial hybrids (KWS9606 VIP3 and NS90 PRO2). This selection allowed for comparisons between genotypes with distinct release histories, where BRS1010 and BRS1055 hybrids represent older hybrids released by Embrapa and KWS9606 VIP3 and NS90 PRO2 represent more recent hybrids. Although none of these hybrids were specifically developed for defoliation tolerance, combining older and newer materials increases the likelihood of detecting contrasting genotypic responses to early leaf removal.

The experiment was arranged in a randomized complete block design with a 4 × 2 factorial scheme, consisting of two factors: (i) genotype (four maize hybrids) and (ii) defoliation (two levels). Defoliation had two levels: (i) defoliated plants, in which all leaves were manually removed at the V4 growth stage using garden shears (cut approximately 5 cm above the soil surface), and (ii) control plants (non-defoliated), which were grown without mechanical intervention (Figure 1).

2.1 | Yield assessment

The development of the plants was evaluated throughout the growth cycle. The number of DAS until emergence and the point at which the ear and tassel reached physiological maturity were recorded. At the end of the maize growth cycle, yield components, including the number, length, weight, and diameter of the ears; the number of rows per ear; the number of kernels per row; grain moisture (G610i moisture meter, Gehaka); and the total grain weight, kernel

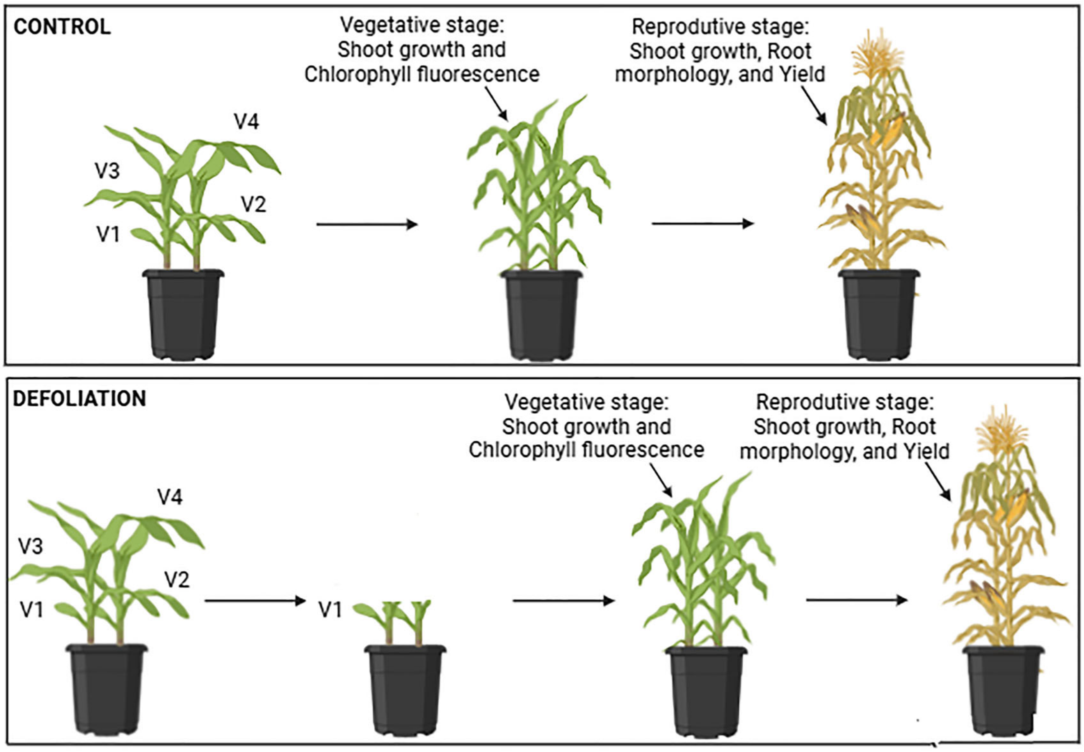

FIGURE 1 Schematic representation of the experimental design comparing control and early defoliation factor levels in maize (*Zea mays* L.). In the control (non-defoliated), plants were grown without mechanical intervention. In the defoliated plants, early defoliation was imposed at the vegetative stage 4 (V4) growth stage by manually removing leaves using garden shears, with the cut made approximately 5 cm above the soil surface. Plant development was assessed across vegetative (shoot growth and chlorophyll fluorescence) and reproductive (shoot growth, root morphology, and yield) stages.

number, and 100-grain weight, were evaluated. The weight of 100 grains was assessed at 13% moisture as follows:

$$\text{Weight of 100 grains} = \frac{\text{Weight of 100 grains} \times (100 - \text{grain moisture})}{87}$$

Additionally, grain yield per plant was calculated as the total grain weight of each plant (total weight per pot divided by 2 plants per pot), and the harvest index (HI) was calculated as follows:

$$\text{HI } (\%) = \frac{\text{Dry mass of grains at 13\% moisture } \times 100}{\text{Total dry plant weight}}$$

2.2 | Canopy structure

The total leaf area (LA) of each plant was assessed at six time points after defoliation: at 8, 11, 19, 22, 35, and 49 days after defoliation (DAD). To calculate the LA, the leaf length, measured from its ligule, was multiplied by the leaf width at the middle third, and a correction factor of 0.75 was applied according to the method of Montgomery (1911).

Plant height and stem diameter of the plants were measured on the same days as the LA evaluations, except for the last assessment. Plant height was determined from the plant's base to the tip of the last fully developed leaf. The stem diameter was measured using a digital caliper at the first internode above the plant base, starting from the soil surface. Shoot dry mass was assessed at the end of the growing cycle. Samples were collected, dried in a forced-air oven (SL-102, Solab) at 65°C until they reached constant weight, and then weighed using an analytical balance (Marte, model AY220). The total plant dry mass was determined as the sum of the shoot dry mass and the root dry mass.

2.3 | Root parameters

For root morphological analysis, the roots were collected at the end of the growing cycle, immediately after harvest. Roots were washed free of soil under running water, and the roots were preserved in 70% ethanol. The roots were scanned using a WinRhizo Arabidopsis software, version 2022 (Regent Instruments), coupled with a professional scanner (LA2400 Scanner, Epson America, Inc., calibrated with Regent Instruments Software) equipped with an additional light unit. The images were used to measure root length, surface area, average diameter, and volume (De Souza et al., 2012). After being scanned, the roots were transferred to a forced-air oven (SL-102, Solab) at 65°C until they reached a constant mass. Biomass was subsequently measured using an analytical balance (Marte, model AY220).

From the previous data, specific root traits, including specific root length (SRL), root fineness (RF), and root tissue density (RTD), were calculated. SRL represents the total root length per unit of dry mass and indicates the plant's capacity to explore the soil for water and nutrients efficiently. RF refers to the ratio between root length and root diameter and reflects the root structural characteristics and potential for soil penetration. RTD is calculated as the root dry mass per unit volume, providing insights into root construction strategies, with higher values indicating denser roots (Zhu et al., 2021).

2.4 | Chlorophyll fluorescence

Chlorophyll fluorescence was evaluated in the morning, between 9:30 a.m. and 11:00 a.m., at three different time points after defoliation: at 9, 17, and 24 DAD. In the defoliated group, measurements were taken from the first fully expanded leaf, corresponding to the V7 leaf, whereas in the control group, the same V7 leaf was selected. Chlorophyll a fluorescence emission was measured using a portable modulated fluorometer (MINI-PAM-II; Heinz Walz). Leaves were dark-adapted for 30 min prior to measurement.

Following dark adaptation, the dark-adapted fluorescence was recorded, and the Fv/Fm ratio (maximum quantum efficiency of PSII) was calculated. Afterward, actinic light was applied for approximately 5 min to stabilize the signal before recording light-adapted parameters. Light-adapted fluorescence measurements were acquired to determine Y(II) (effective photochemical quantum yield of PSII), qP (photochemical quenching), NPQ (nonphotochemical quenching), Y(NPQ) (quantum yield of regulated nonphotochemical energy dissipation of PSII), and Y(NO) (quantum yield of nonregulated nonphotochemical energy dissipation of PSII) (Maxwell & Johnson, 2000). All values were automatically computed by the device's software using standard equations that integrate both dark- and light-adapted fluorescence data. (Supporting Information Data).

Fv/Fm indicates the maximum potential photochemical efficiency of PSII and was used to verify whether early defoliation compromised the integrity of the photosynthetic apparatus. Y(II) represents the effective PSII quantum yield under light and therefore directly reflects the plant's capacity to convert absorbed light into photosynthesis after leaf removal. qP describes the degree of reaction center openness, allowing us to identify whether genotypes maintained a greater ability to use incoming energy under defoliation. NPQ quantifies the proportion of excess energy dissipated in a controlled manner as heat, functioning as a protective mechanism when LA is reduced. Y(NPQ) complements this assessment by expressing the fraction of energy dissipated through regulated pathways, whereas Y(NO) indicates the portion lost through nonregulated routes, often associated with physiological limitations or photoinhibition. Together, these parameters reveal whether defoliation led to a redistribution of absorbed light among photochemistry, protective dissipation, and energy losses, helping distinguish genotypes that remained more efficient and less sensitive to the stress imposed by early leaf removal.

2.5 | Statistical analysis

The data collected were subjected to descriptive statistical analysis, using means and standard deviations. Correlation analyses were performed among measured parameters.

2.5.1 | Inferential analysis for single-time-point traits

Analysis of variance (ANOVA) was conducted to evaluate significant differences between groups, followed by the Scott–Knott clustering test to identify significant clusters. Only variables with significant interactions are reported and discussed. All analyses were performed in Sisvar (version 5.8, build 92), with a significance level of $p < 0.05$. For the final LA measurement at 49 DAD, statistical analysis was conducted using ANOVA followed by the Scott–Knott test to compare the factors.

2.5.2 | Inferential analysis for repeated-measures traits

Chlorophyll fluorescence traits were analyzed in long data format with fixed factors of genotype (four levels), defoliation (two levels), and time (9, 17, and 24 DAD; categorical). Analyses were performed in R (version 4.5.1). Data handling and visualization used the "tidyverse" packages (*dplyr*, *tidyr*, *ggplot2*). Replicates were arranged as blocks; therefore, replicate and block are equivalent in the design. Because the same pot (genotype × defoliation × replicate) was measured across time points, pot was treated as the repeated subject.

For each trait, a linear mixed-effects model was fitted with all fixed-effect interactions and a random intercept for pot:

$$\text{response} \sim \text{genotype} \times \text{defoliation level} \times \text{time} + (1 \mid \text{pot})$$

Models were fitted by restricted maximum likelihood using the "lme4"/"lmerTest" packages. Tests of fixed effects used the "Satterthwaite" approximation for denominator degrees of freedom. Significance was assessed at $\alpha = 0.05$.

At each time point, estimated marginal means (EMMs) for all genotype × defoliation combinations were obtained with the "emmeans" package. Pairwise comparisons among EMMs were evaluated with Tukey's honestly significant difference adjustment. Compact letter displays were generated independently for each time point using "multcomp::cld" (groups sharing a letter were not significantly different at $\alpha = 0.05$). When degrees of freedom differed across contrasts, "emmeans" applied Sidak adjustment automatically. Model assumptions (residual normality, homoscedasticity, and influential values) were verified using diagnostic plots.

Regression analysis of LA over time was performed for each genotype using Graph Pad Prism, with the resulting equations used to evaluate growth trends.

2.5.3 | Multivariate exploratory analysis—Principal component analysis

Principal component analysis (PCA) was performed using the "prcomp ()" function in R (version 4.4.3) to explore multivariate patterns of variation across genotypes and defoliation levels. Prior to analysis, all the response variables were scaled to unit variance and centered mean, and PCA was conducted on the correlation matrix. The first two principal components (first principal component [PC1] and second principal component [PC2]) were retained for interpretation based on the proportion of variance explained. Two graphical outputs were generated using the "fact extra" and "ggplot2" packages: a score plot and a biplot. Shapes represent genotypes, and colors indicate combined genotype–defoliation groups, allowing visual separation and pattern recognition among experimental conditions.

3 | RESULTS

3.1 | Growth and yield traits under early defoliation

Early defoliation reduced the shoot growth parameters but did not affect grain yield. No significant interaction ($p > 0.05$) was detected between the genotype and defoliation for any of the yield components (Table 1). Seven traits, namely, ear weight, ear length, grains per row, ear diameter, total grain weight, kernel number, and grain yield, remained unaffected by defoliation, with no significant differences between the control and defoliated plants.

TABLE 1 Analysis of variance (ANOVA) results indicating the significance of factor I (BRS1010, BRS1055, KWS9606 VIP3, and NS90 PRO2), factor II (defoliated plants and control/non-defoliated plants), and the interaction between these factors for yield-related traits in maize genotypes experiencing early defoliation (vegetative stage 4 [V4]) or not (control).

Parameter	Factor I	Factor II	Interaction
ASI	ns	*	ns
Ear diameter	*	ns	ns
Ear length	*	ns	ns
Ears per plant	ns	*	ns
Ear weight	ns	ns	ns
Grain weight	*	ns	ns
Grain yield	*	ns	ns
Harvest index	ns	*	ns
Kernels per row	ns	ns	ns
Kernel number	ns	ns	ns
Leaf area	ns	*	ns
Open anthers	*	*	ns
Plant height	*	*	ns
Rows per ear	*	*	ns
Stem diameter	*	*	ns
Total dry mass	ns	*	ns
100-grain weight	*	*	ns

Note: Asterisks indicate statistical significance, and ns indicates non-significance according to the Scott–Knott test ($p < 0.05$).
Abbreviation: ASI, anthesis–silking Interval.

In contrast, defoliation led to significant reductions in plant height, stalk diameter, LA, dry mass, the number of rows per ear, and the number of ears per plant across all genotypes (Table 1 and Table S2). The 100-grain weight was also lower in defoliated plants. Compared with controls, however, the HI increased, and tassel emergence was delayed (Table 1).

The LA consistently decreased in response to defoliation across all genotypes. Regression analysis revealed a similar linear trend in LA reduction for BRS1010, BRS1055, and NS90 PRO2, whereas KWS9606 VIP3 exhibited a shallower slope under control conditions. Under defoliation, however, the LA of KWS9606 VIP3 followed a trend comparable to that of the other genotypes. Among the four genotypes, compared with their respective controls, BRS1010 and BRS1055 presented the greatest reduction in LA under defoliation (Figure 2a,b).

3.2 | Root morphology and biomass allocation following defoliation

Defoliation reduced root dry mass in all the genotypes, but the extent of this reduction varied among them. While root dry weight did not differ between genotypes under control

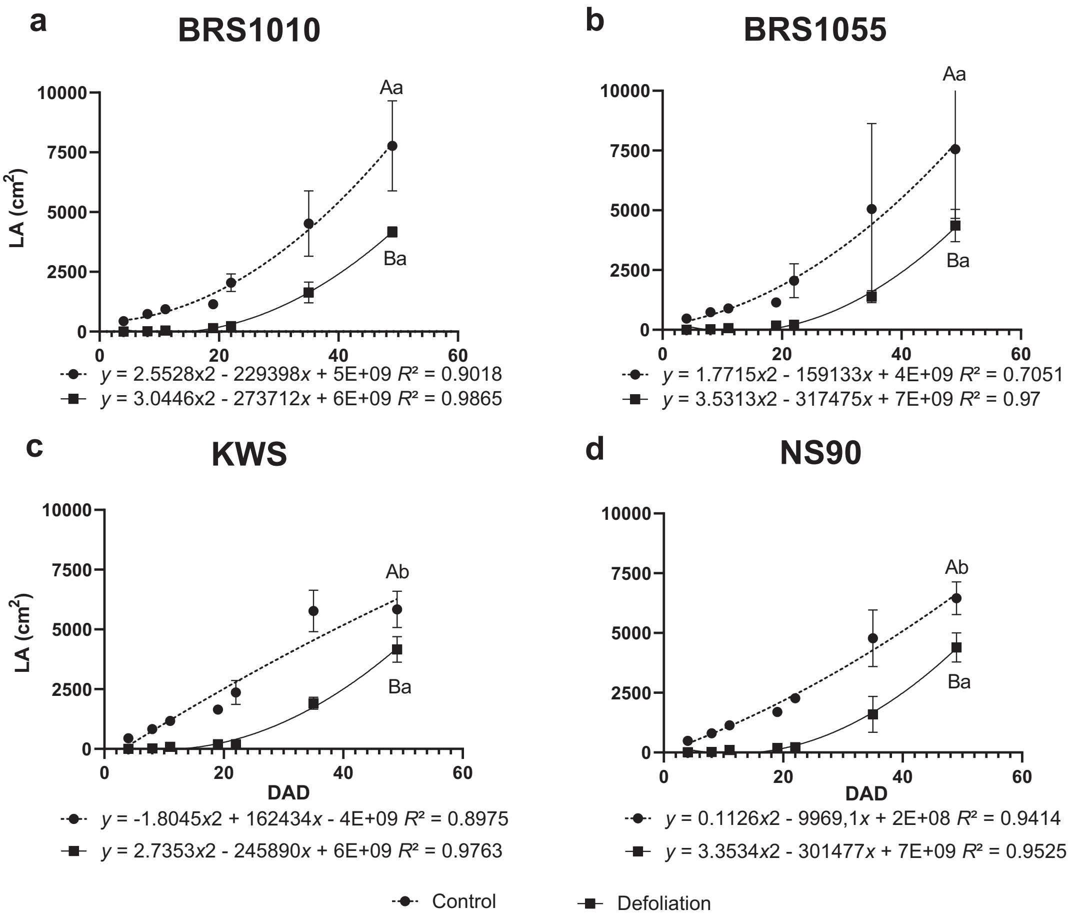

FIGURE 2 Changes in total leaf area (LA) as a function of the days after defoliation (DAD) for four maize genotypes (BRS1010, BRS1055, KWS9606 VIP3, and NS90 PRO2) in plants experiencing early defoliation or not (control). Different uppercase letters indicate differences between the control and defoliation plants, whereas different lowercase letters indicate differences across genotypes according to the Scott–Knott test ($p < 0.05$) on the basis of the result of a significant interaction.

conditions, compared with BRS1010 and NS90 PRO2 plants, KWS9606 VIP3 and BRS1055 plants retained significantly greater root dry weight (Figure 3).

RF remained unchanged between factors II, whereas RTD increased in response to defoliation (Table S2). The other root morphological traits, including root length, surface area, and volume, were lower in the defoliated plants across all the genotypes than in their respective controls (Table 2).

3.3 | Chlorophyll fluorescence responses to defoliation across genotypes and time

Defoliation affected chlorophyll fluorescence parameters in a genotype-dependent manner across the evaluation dates (9, 17, and 24 DAD). Each chlorophyll fluorescence parameter showed significant differences ($p < 0.05$) at least at one evaluation date, indicating heterogeneous responses across genotypes (Table 3).

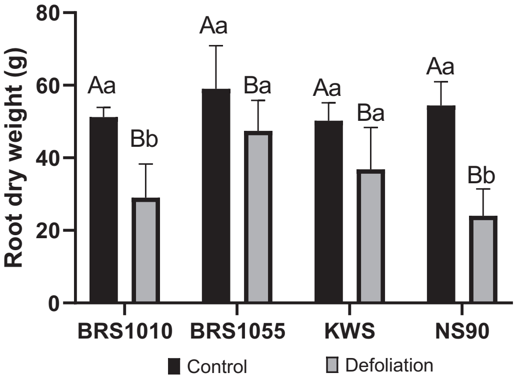

FIGURE 3 Root dry weight at the end of the growing season for four maize genotypes (BRS1010, BRS1055, KWS9606 VIP3, and NS90 PRO2) in plants experiencing early defoliation or not (control). Different uppercase letters indicate differences between the control and defoliation plants, whereas different lowercase letters indicate differences across genotypes according to the Scott–Knott test ($p < 0.05$).

TABLE 2 Analysis of variance (ANOVA) showing the proportion of variance explained by factor I (BRS1010, BRS1055, KWS9606 VIP3, and NS90 PRO2), factor II (defoliated plants and non-defoliated plants), and the interaction between these factors for root traits in maize genotypes experiencing early defoliation or not (control).

Parameter	Factor I	Factor II	Interaction
AVG diameter	*	*	ns
L thick	*	*	ns
L thin	*	*	ns
L very thin	*	*	ns
Length cm	*	*	ns
Root dry weight	*	*	*
Root fineness	ns	ns	ns
Root tissue density	ns	*	ns
Root volume	*	*	ns
SA thick	*	*	ns
SA thin	*	*	ns
SA very thin	*	*	ns
Specific root length	*	*	ns
Surface area	*	*	ns
V thick	*	*	ns
V thin	*	*	ns
V very thin	*	*	ns

Note: AVG diameter = average root diameter; L thick = length of thick roots (>2 mm); L thin = length of thin roots (0.5–2 mm); L very thin = length of very thin roots (<0.5 mm); Length cm = total root length; Root dry weight = root biomass after drying; Root fineness = root length per unit of dry weight; Root tissue density = root dry weight per unit of volume; Root volume = total root volume; SA thick = surface area of thick roots (>2 mm) (cm^2); SA thin = surface area of thin roots (0.5–2 mm); SA very thin = surface area of very thin roots (<0.5 mm); Specific root length = root length per unit of root mass; Surface area = total root surface area; V thick = volume of thick roots (>2 mm) (cm^3); V thin = volume of thin roots (0.5–2 mm); V very thin = volume of very thin roots (<0.5 mm). Asterisks indicate statistical significance, and ns indicates non-significance effect according to the Scott–Knott test ($p < 0.05$).

TABLE 3 Within-time multiple comparisons among genotype × defoliation combinations (four maize genotypes: BRS1010, BRS1055, KWS9606 VIP3, and NS90 PRO2; two defoliation levels: Defoliated and control non-defoliated) for chlorophyll fluorescence parameters based on estimated marginal means (EMMs), adjusted using the Sidak method.

Parameter	9 DAD	17 DAD	24 DAD
Fv/Fm	ns	ns	*
NPQ	*	*	ns
qP	*	*	*
Y (II)	*	ns	ns
Y (NPQ)	*	*	*

Note: Fv/Fm, maximum quantum efficiency of PSII; NPQ, nonphotochemical quenching; qP, photochemical quenching; Y(II), effective quantum yield of PSII; Y(NPQ), quantum yield of nonphotochemical energy dissipation in PSII. DAD, days after defoliation. Asterisks indicate statistical significance ($p < 0.05$), and ns = not significant ($p > 0.05$).

At 9 DAD, significant differences between control and defoliated plants were detected. Y(II) was higher under defoliation in KWS9606 VIP3 (Figure 4g), whereas qP was higher under defoliation in BRS1010 (Figure 4i). NPQ and Y(NPQ), control plants resulted in higher values than defoliated plants for BRS1010 and KWS9606 VIP3 (Figure 4m,o,q,s). No differences between control and defoliation were observed for Fv/Fm in any genotype (Figure 4a–d).

At 17 DAD, qP responses diverged by genotype: in BRS1010, control values were higher than defoliation, whereas in KWS9606 VIP3, defoliation exceeded control (Figure 4i,k). For NPQ, BRS1055 control exhibited higher values than defoliation (Figure 4n). Fv/Fm, Y(II), and Y(NPQ) showed no control–defoliation differences within any genotype (Figure 4a–h, q–t).

At 24 DAD, genotype × defoliation level combinations effects were limited to qP: in both BRS1010 and KWS9606 VIP3, defoliation produced higher qP than control (Figure 4i,k). The remaining traits, Fv/Fm, Y(II), NPQ, and Y(NPQ), showed no within-genotype control–defoliation differences (Figure 4a–h, m–t).

3.4 | PCA of integrated morphological and physiological traits under defoliation

The PC1 had an eigenvalue of 17.2, accounting for 30.18% of the total variance in the dataset. The PC2 had an eigenvalue of 6.53, explaining 11.46% of the variance (Figure 5c). Together, PC1 and PC2 captured 41.64% of the total variation observed in the data (Figure 5d). PC1 was predominantly influenced by morphological parameters, particularly root-related traits and some aerial traits, whereas PC2 was driven by physiological parameters and aerial morphological traits based on variable loadings (Figure 5b).

Parameters including Y(II) at 9 and 24 DAD, Fv/Fm, the quantum yield of nonregulated heat dissipation and fluorescence emission [Y(NO)] at 9 DAD, qP, and qL at 24 DAD, as well as the HI and days to tassel emergence, exhibited negative loadings on PC1. These variables were positively correlated with defoliation, indicating that they were favored under these conditions. Conversely, variables with positive loadings on PC1, including the root surface area, surface area of fine roots (SA thin), and length of fine roots (L thin), were strongly associated with the control condition (Figures 5a,b).

On PC2, the parameters with the highest positive loadings included the NPQ capacity and quantum yield of regulated energy dissipation [Y(NPQ)] at 9 DAD, with loadings ranging from 0.57 to 0.71. In contrast, grain yield, total grain weight (PTG13), and Y(II) at 9 DAD had the greatest negative loadings on PC2, with values between −0.61 and −0.65. Notably, the photochemical efficiency of PSII was the only parameter that negatively influenced both PC1 and PC2 (Figure 5b).

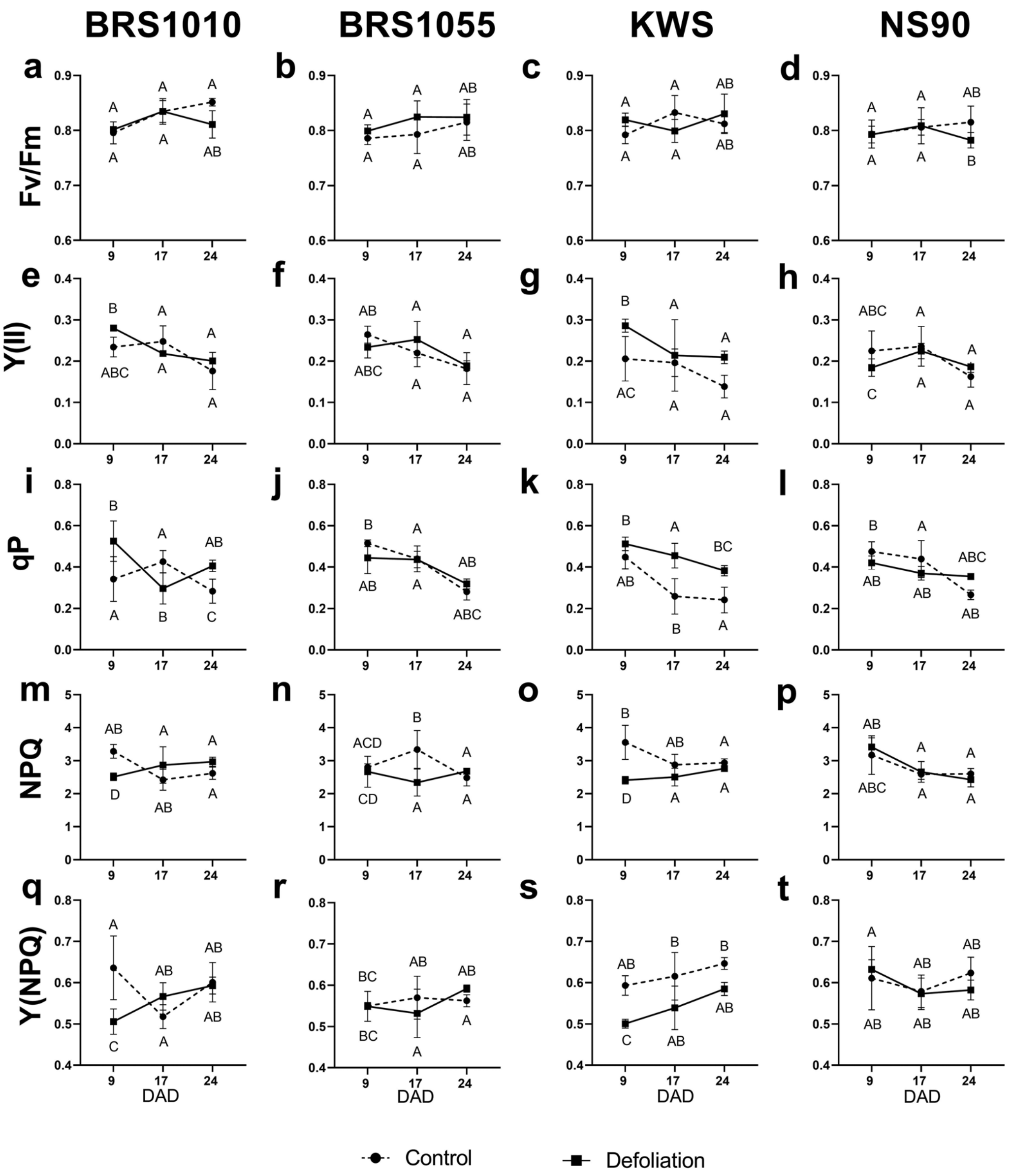

FIGURE 4 Chlorophyll fluorescence parameters in four maize genotypes (BRS1010, BRS1055, KWS9606 VIP3, and NS90 PRO2) under control (non-defoliated) and defoliated conditions across 9, 17, and 24 days after defoliation (DAD). Fv/Fm, maximum quantum efficiency of PSII; NPQ, nonphotochemical quenching; qP, photochemical quenching; Y(II), effective quantum yield of PSII; Y(NPQ), quantum yield of nonphotochemical energy dissipation in PSII; and DAD, days after defoliation. Means followed by different letters within each sampling time (9, 17, or 24 DAD) differ significantly among genotype × defoliation combinations according to pairwise comparisons of estimated marginal means (EMMs), adjusted by the Sidak method at $p < 0.05$.

4 | DISCUSSION

The absence of significant effects on yield components indicates that tolerance of maize genotypes to early defoliation stress may occur. This absence of interaction indicates that both older (BRS1010 and BRS1055) and modern (KWS9606 VIP3, and NS90 PRO2) hybrids maintained similar tolerance to early defoliation, suggesting that this trait has been consistently maintained throughout the genetic improvement of maize in Brazil. Such tolerance aligns with earlier reports demonstrating that grain yield in maize is not significantly affected by defoliation occurring early in plant development (Blanco et al., 2023). For instance, Pearson and Fletcher (2009) reported that defoliation up to growth stage V4 had a minimal effect on grain yield. These mechanisms may involve resource reallocation and metabolic adjustments that enable plants to maintain growth and grain production despite leaf loss (Ferreira et al., 2024).

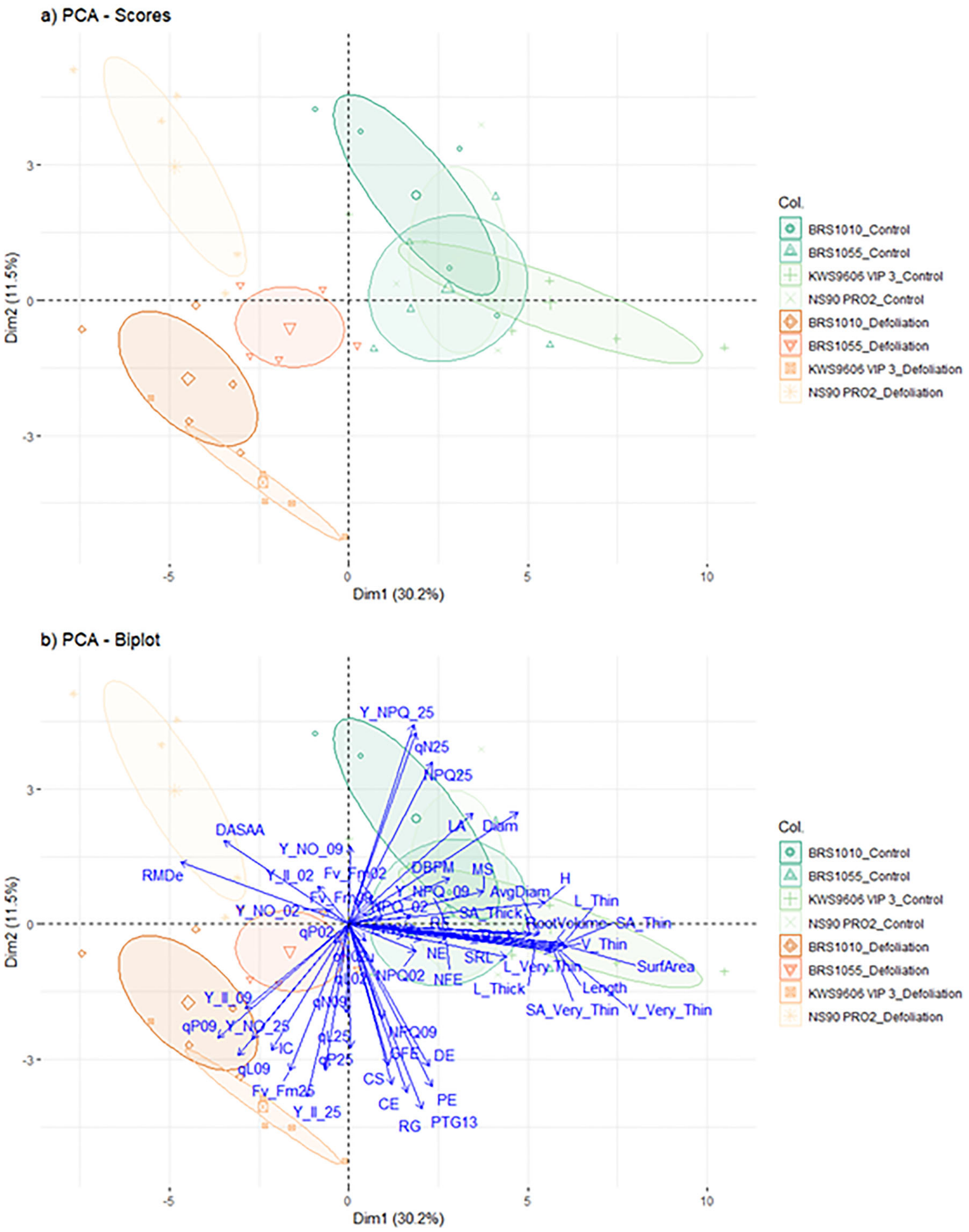

FIGURE 5 Principal component analysis (PCA) of maize genotypes grown under early defoliation and control (non-defoliation) conditions. PCA was performed to identify the variation in the data after filtering by factors. (a) Score plot showing the distribution of samples across first principle component (PC1) and second principal component (PC2); ellipses indicate 95% confidence intervals based on the multivariate *t* distribution. (b) Biplot displaying correlations between original variables and principal components.

This study was conducted in a single season, regarding the stability of these compensatory responses across years should be made with caution. Although the experimental design ensured adequate within-season replication, multi-year repetition would strengthen statistical inference and help determine whether the observed genotypic differences remain consistent under varying environmental conditions. Future studies should incorporate temporal replication and further identify genotypes with contrasting responses to early defoliation, improving the selection of experimental materials and the interpretation of treatment effects. In addition, research could further investigate the underlying mechanisms of tolerance by examining genotypic variability in traits that contribute to compensatory growth.

The results for the growth parameters, particularly the LA regression, provide further insights into the responses of maize to defoliation. The consistent reduction in LA and total biomass under defoliation reflects a resource-conservation response, in which energy and assimilates are reallocated primarily toward the maintenance of essential metabolism rather than structural development. As a result, even with reduced LA and biomass, plants are still able to progress toward reproductive development, although at the cost of the structural growth observed in control plants. Similar patterns have been reported in previous studies, where reduced biomass in defoliated plants were associated with physiological trade-offs consistent with stress compensation mechanisms (Jahan et al., 2022). Regression analysis confirmed a progressive decline in LA among the defoliated genotypes, although the KWS9606 VIP3 hybrid exhibited a milder reduction, indicating less sensitivity under defoliation while maintaining key physiological processes. Research on stay-green traits further supports this pattern, indicating that genotypes capable of retaining functional LA under stress tend to maintain photosynthetic performance and reduce yield penalties (Christopher et al., 2016).

These results emphasize the importance of LA dynamics in determining plant performance under stress. The reduction in LA due to defoliation was primarily associated with the removal of basal leaves. Although we did not directly assess photosynthetic efficiency, our inferences rely on chlorophyll fluorescence parameters, which can provide indirect indicators of PSII efficiency. The literature indicates that lower canopy leaves generally contribute less to net carbon assimilation due to shading and age-related decline (Wu et al., 2022). These leaves may also increase water loss through transpiration. In our study, however, such effects were not measured directly, and the greenhouse conditions likely reduced shading compared with field environments. Nevertheless, the consistent reduction in basal LA under defoliation may help explain why defoliated plants improved responses under stress, particularly in water-limited environments.

Other studies have also shown that partial defoliation, such as removal of upper or lateral leaves, can enhance grain yield under drought by improving resource use efficiency (Zheng et al., 2021). Although our study involved complete basal defoliation at V4, which represents a different physiological context, these findings illustrate the broader principle that reducing LA can, under certain conditions, contribute to adaptive stress responses. While this mechanism was not investigated in our experiment, acknowledging it provides useful context when comparing different defoliation strategies and their potential physiological outcomes. This relationship also represents a promising avenue for future studies aiming to explore whether early defoliation may influence plant performance under water-limited conditions.

The reduction in plant weight observed in defoliated maize further highlights the impact of early leaf removal on growth dynamics. Consistent with previous findings, the decrease in plant biomass under defoliation conditions is attributed primarily to morphological adjustments that limit structural expansion (Xu et al., 2023). In our study, the significant reductions in height in defoliated plants suggest a possible shift in resource allocation toward metabolic maintenance, rather than continued vegetative growth, under greenhouse conditions. This aligns with the observed trends in biomass accumulation, reinforcing the notion that defoliation-induced stress triggers adaptive responses aimed at optimizing survival rather than maximizing plant size. Such findings underscore the complex interaction between physiological and structural responses in shaping maize tolerance to foliar loss.

In addition to these structural trade-offs, early defoliation may influence agronomic traits related to plant stability. Recent studies have demonstrated that early-stage defoliation may have beneficial effects on lodging resistance in maize. Xu et al. (2023) reported that defoliation at the seedling stage resulted in shorter plants with a lower center of gravity, reducing their susceptibility to lodging under adverse weather conditions. These findings suggest that while early leaf loss may impose initial growth limitations, it can also increase structural stability, mitigating yield losses caused by mechanical instability. The reduction in plant height observed in defoliated maize further supports this hypothesis, indicating that targeted defoliation strategies could be leveraged to improve standability in high-density planting systems or regions prone to strong winds. This pattern underscores the dual nature of defoliation effects, where physiological trade-offs can sometimes confer adaptive advantages depending on the environmental context and management practices.

These aboveground responses appear to be accompanied by corresponding changes in root system architecture. The significant interactions between factors for root dry mass underscore the sensitivity of root systems to defoliation stress. The observed reduction in root biomass among defoliated genotypes, coupled with increased RTD, suggests structural adaptations aimed at maintaining resource acquisition under adverse conditions. A higher RTD indicates that the roots become denser, with more biomass allocated per unit of root volume. This adaptation reflects a shift toward more compact, resource-conservative root structures (Le Stradic et al., 2021). Moreover, increased RTD is typically associated with increased root longevity and stress tolerance but a reduced capacity for water and nutrient uptake (Freschet et al., 2010; Ryser, 1996; Weemstra et al., 2016).

The increase in RTD observed in defoliated plants, together with the reduction in SRL, indicates a shift toward thicker and denser roots. Such roots typically contain a higher proportion of lignified tissues, making them more costly to build but more durable and mechanically robust. Although these roots do not lose their absorptive capacity entirely, their anatomical characteristics generally confer lower efficiency per unit mass while enhancing structural reinforcement. This tendency aligns with the observed improvements in lodging resistance following early-stage defoliation, suggesting that denser root systems may contribute to increased anchorage and mechanical stability. It is important to note, however, that brace roots, another critical component of anchorage in maize, were not evaluated in this study. Therefore, any direct conclusions regarding lodging resistance should be made cautiously, and future work should examine whether defoliation influences brace root development as part of this adaptive response.

Although defoliation initially limits plant growth, it may promote a root system that helps mitigate lodging risks in high-density planting systems or wind-prone environments. Further studies are needed to evaluate whether such effects extend to field conditions, including high-density systems. These findings emphasize the trade-offs between shoot and root development, where plants shifted their resource allocation to sustain growth and tolerance under challenging conditions (Gao et al., 2023).

Furthermore, a study by Y. Liu et al. (2023) revealed that both defoliation and fertilization increase the influence of root traits on soil properties, particularly aggregate stability, highlighting the crucial role of root-mediated processes in soil health and tolerance. They reported that although the amplitude of root trait responses to defoliation varied among species, the direction of changes remained consistent. Specifically, defoliation increased SRL while reducing root biomass, root mass density (RMD), and root length density, reflecting a trade-off between root expansion and resource conservation strategies. In alignment with these findings, our results also revealed a reduction in root biomass following defoliation, while RMD was not evaluated in the present study. The increased RTD further supports this adaptive shift toward structural reinforcement, which favors root persistence under stress conditions.

The photochemical and nonphotochemical parameters measured after defoliation provide information on genotype-specific responses to leaf loss, emphasizing the dynamic nature of photosynthetic adjustments under stress. Although gas exchange was not measured, the chlorophyll fluorescence data allow a nondestructive assessment of PSII efficiency and energy partitioning. The Fv/Fm values remained close to 0.8 across all the genotype × defoliation level combinations, suggesting that PSII remained largely functional and that defoliation did not cause major photoinhibition. However, it is important to note that Fv/Fm may not always be sensitive to early or moderate stress signals, as reported in drought and high-temperature studies (Brestic & Zivcak, 2013; Souza et al., 2013).

High NPQ values were observed even in the absence of photoinhibition. Similar dissociations between Fv/Fm and NPQ have been reported, emphasizing that NPQ can vary substantially due to regulatory adjustments, even under conditions without changes in Fv/Fm or evident stress (Brestic & Zivcak, 2013; W.-J. Liu et al., 2022). This underscores the importance of complementing dark-adapted parameters such as Fv/Fm with light-adapted traits (e.g., qP, Y(II), and NPQ) to capture dynamic aspects of PSII regulation. Taken together, these patterns suggest that although PSII remained operational, some genotypes may have activated regulatory mechanisms to dissipate excess energy, possibly as a regulatory adjustment to maintain photosynthetic stability.

At 9 DAD, KWS9606 VIP3 exhibited higher Y(II) under defoliation, and qP was higher in both KWS9606 VIP3 and BRS1010, indicating greater openness of PSII centers. NPQ did not differ significantly between defoliation levels in KWS9606 VIP3, although values tended to remain elevated even in control plants. This parallel pattern of relatively high NPQ together with high qP under non-stressed conditions is unusual, since qP is generally high and NPQ low in such contexts. This raises the question of whether KWS9606 VIP3 displays a genotype-specific regulatory mode in which both photochemical and nonphotochemical pathways remain active simultaneously, even without clear external stress triggers. While the physiological basis of this behavior remains unclear, it highlights variation in how genotypes balance energy use and dissipation.

Interestingly, under control conditions in KWS9606 VIP3, both qP and NPQ remained elevated, which is not commonly observed in non-stressed plants. This simultaneous increase in photochemical and nonphotochemical pathways may reflect a genotype-specific anticipatory adjustment, potentially enhancing energy management and photoprotection even in the absence of strong external stress cues. While the physiological basis for this dual activation remains unclear, similar patterns have been observed in other crops under mild or transient stress conditions (Bhusal et al., 2021).

These results are aligned with those of previous studies showing that maize genotypes can maintain PSII efficiency under moderate stress through physiological acclimation (Bashir et al., 2021; Chisonga et al., 2023). Further studies are needed to clarify whether such responses are related to developmental timing, internal resource status, or subtle stress signals not detectable through conventional parameters. We acknowledge this uncertainty in the current dataset and highlight this pattern as an open question for future investigation.

Conversely, BRS1055 exhibited a more conservative pattern, with modest changes in fluorescence parameters. NPQ values were consistently higher in the control at 9 and 17 DAD. However, the absolute differences were small and may reflect limited biological impact. This pattern suggests that photoprotective responses in BRS1055 may occur more passively or with a delayed onset under defoliation. By 24 DAD, NPQ values no longer differed, indicating that any initial adjustments had stabilized. These genotype-specific trends highlight the variation in photosynthetic resilience and flexibility. Similar trends have been observed in drought-tolerant maize genotypes, in which PSII efficiency is sustained through photochemical adjustments rather than a reliance on thermal dissipation (Guo et al., 2020).

Interestingly, NS90 PRO2 exhibited a divergent response compared to other genotypes. Exhibiting no significant differences in chlorophyll fluorescence parameters between defoliated and control plants across all time points. This lack of responsiveness suggests limited physiological adaptation in this genotype, possibly reflecting a more conservative or stable photosynthetic behavior under early defoliation stress.

The dynamics of NPQ and Y(NPQ) further illustrate genotype-specific photoprotective strategies. At 9 DAD, NPQ was greater in the control plants than in the defoliated plants for BRS1010 and KWS9606 VIP3, suggesting that these non-defoliated genotypes dissipated more excess light energy. These findings indicate that different genotypes prioritize either photochemical or nonphotochemical pathways to prevent photodamage under prolonged stress (Derks et al., 2015).

The results contribute to a broader understanding of how maize genotypes respond to defoliation, reinforcing the notion that genotype-specific strategies influence photosynthetic resilience. While some genotypes, such as KWS9606 VIP3 and BRS1010, increase PSII efficiency under defoliation, others, such as BRS1055, rely on delayed photoprotective mechanisms. These findings align with reports that maize exhibits high plasticity in response to defoliation, with certain genotypes compensating for leaf loss through improved light utilization rather than through strict photoprotective pathways (Chisonga et al., 2023). Furthermore, these genotype-specific responses highlight the potential for targeted breeding strategies to increase stress tolerance in maize. Nevertheless, it is important to acknowledge that fluorescence-based measurements provide indirect assessments of photosynthetic performance and cannot replace direct gas exchange analyses such as CO_2 assimilation or stomatal conductance.

Overall, these results provide critical insights into physiological mechanisms underlying the ability of maize to tolerate defoliation. The observed trends emphasize the importance of genotype selection in optimizing photosynthetic efficiency under stress conditions, contributing to improved crop management strategies and tolerance to environmental challenges. Future research should further explore the genetic and metabolic bases of these responses, integrating molecular and physiological approaches to refine genotype selection for stress tolerance in maize production systems.

These findings align with previous research on abiotic stress responses, where reductions in Y(II) under drought, heat, or nutrient limitations are typically associated with impaired photochemical activity (Keya et al., 2025; Salika & Riffat, 2021). Similarly, drought stress has been shown to significantly decrease Y(II) while increasing Y(NO) and Y(NPQ), emphasizing the sensitivity of PSII to environmental stress and the necessity of energy dissipation mechanisms to protect the photosynthetic apparatus (Guo et al., 2020). Interestingly, in the present study, some genotypes, particularly KWS9606 VIP3 and BRS1010, presented increased Y(II) after defoliation, suggesting an adaptive advantage that enhances photosynthetic efficiency despite reduced LA. This ability to maintain or even improve PSII performance under stress is crucial for sustaining growth and productivity. Moreover, studies on pest-induced defoliation have indicated that maize plants exhibit considerable tolerance to leaf loss, with minimal effects on grain yield, reinforcing the hypothesis that maize can effectively compensate for defoliation stress (Chisonga et al., 2023). Additionally, the differences in NPQ responses observed suggest that genotypes exhibit distinct photoprotective mechanisms, with some genotypes prioritizing photochemical energy use and others relying more on nonphotochemical dissipation to avoid excess excitation pressure (Bashir et al., 2021).

Finally, PCA revealed that PC1 was primarily associated with morphological and root parameters, offering critical insights into how these traits respond to defoliation and control conditions. Under control (non-defoliated) conditions, root development and structural growth, such as root dry weight, surface area, and volume, were strongly associated with PC1, highlighting the importance of belowground resource allocation in the optimization of nutrient and water uptake. This aligns with findings that robust root systems enhance productivity by maximizing resource acquisition (Gao et al., 2023). In defoliated plants, however, the reduction in root development observed in PC1 suggests a strategic reallocation of resources for shoot recovery and maintenance of photosynthetic function, further reinforcing the trade-off between aboveground and belowground growth (Ferreira et al., 2024).

PC2 was influenced primarily by physiological parameters, particularly those related to PSII efficiency, such as Y(II) and NPQ, highlighting the critical role of these traits under defoliation stress. The greater contribution of these parameters to PC2 underscores the adaptability of genotypes BRS1010 and KWS9606 VIP3 in managing energy production and dissipation during stress conditions. The genotypes that exhibited greater Y(II) values under defoliation maintained higher photochemical efficiency, which is essential for sustaining photosynthetic activity despite reduced LA. Moreover, variations in NPQ reflect different photoprotection strategies, with some genotypes prioritizing energy dissipation to prevent photodamage. These findings suggest that PC2 captures physiological adjustments critically for maintaining functional photosynthesis under defoliation stress, offering key insights into the mechanisms driving genotype tolerance. Understanding these traits can guide the identification of genotypes better suited to cope with environmental challenges, strengthening breeding programs targeting photosynthetic efficiency and stress tolerance.

5 | CONCLUSION

This study demonstrated that early defoliation did not significantly affect maize grain yield, underscoring the tolerance of the evaluated genotypes to foliar loss. Although defoliation induced measurable alterations in morphological traits and elicited genotype-specific shifts in chlorophyll fluorescence parameters, none of these physiological adjustments translated into yield penalties. The results highlight the capacity of maize genotypes to deploy distinct, yet functionally effective, compensatory mechanisms that safeguard productivity under early vegetative stress.

AUTHOR CONTRIBUTIONS

Danielle de Oliveira: Data curation; formal analysis; investigation; methodology; visualization; writing—original draft; writing—review and editing. **Daniele Maria Marques**: Data curation; formal analysis; methodology; writing—review and editing. **Yago Afonso Castro**: Data curation; formal analysis. **Paulo César Magalhães**: Investigation; writing—original draft. **Émerson Borghi**: Investigation; writing—original draft. **Decio Karam**: Investigation; writing—original draft. **Plinio Rodrigues dos Santos Filho**: Conceptualization; formal analysis; investigation. **Amanda A. Cardoso**: Conceptualization; formal analysis; methodology; validation; visualization; writing—original draft. **Thiago Corrêa de Souza**: Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing—original draft; writing—review and editing.

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository at: https://doi.org/10.5061/dryad.z8w9ghxtc.

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REFERENCES

Alvarez, V. V. H., & Ribeiro, A. C. (1999). *Fertility of soils: Interpretation of chemical analyses and recommendations for fertilization and liming* [Fertilidade de solos: interpretação de análises químicas e recomendações de adubação e calagem]. Comissão de Fertilidade do Solo do Estado de Minas Gerais.

Bashir, N., Athar, H.-U.-R., Kalaji, H. M., Wróbel, J., Mahmood, S., Zafar, Z. U., & Ashraf, M. (2021). Is photoprotection of PSII one of the key mechanisms for drought tolerance in maize? *International Journal of Molecular Sciences*, *22*(24), 13490. https://doi.org/10.3390/ijms222413490

Bhusal, B., Poudel, M. R., Pandit, R., Regmi, R., Neupane, P., Bhattarai, K., Maharjan, B., KC, B., & Acharya, S. (2021). A review on abiotic stress resistance in maize (*Zea mays* L.): Effects, resistance mechanisms and management. *Journal of Biology and Today's World*, *10*(2), 1–3. https://doi.org/10.35248/2322-3308.21.10.006

Blanco, C. A., Hernandez, G., Conover, K., Dively, G. P., Nava-Camberos, U., Portilla, M., Abel, C. A., Williams, P., & Hutchison, W. D. (2023). Severe defoliation of vegetative maize plants does not reduce grain yield: Further implications with action thresholds. *Southwestern Entomologist*, *48*(4), 791–804. https://doi.org/10.3958/059.048.0404

Blanco, C. A., Hernandez, G., Valentini, G., Portilla, M., Abel, C. A., Williams, P., Nava-Camberos, U., Hutchison, W. D., & Dively, G. P. (2022). Grain yield is not impacted by early defoliation of maize: Implications for fall armyworm action thresholds. *Southwestern Entomologist*, *47*(2), 335–344. https://doi.org/10.3958/059.047.0209

Brestic, M., & Zivcak, M. (2013). PSII fluorescence techniques for measurement of drought and high temperature stress signal in crop plants: Protocols and applications. In *Molecular stress physiology of plants* (pp. 87–131). Springer. https://doi.org/10.1007/978-81-322-0807-5_4

Cairns, J. E., & Prasanna, B. M. (2018). Developing and deploying climate-resilient maize varieties in the developing world. *Current Opinion in Plant Biology*, *45*, 226–230. https://doi.org/10.1016/j.pbi.2018.05.004

Chisonga, C., Chipabika, G., Sohati, P. H., & Harrison, R. D. (2023). Understanding the impact of fall armyworm (*Spodoptera frugiperda* J. E. Smith) leaf damage on maize yields. *PLoS One*, *18*(6), e0279138. https://doi.org/10.1371/journal.pone.0279138

Christopher, J. T., Christopher, M. J., Borrell, A. K., Fletcher, S., & Chenu, K. (2016). Stay-green traits to improve wheat adaptation in well-watered and water-limited environments. *Journal of Experimental Botany*, *67*(17), 5159–5172. https://doi.org/10.1093/jxb/erw276

Derks, A., Schaven, K., & Bruce, D. (2015). Diverse mechanisms for photoprotection in photosynthesis: Dynamic regulation of photosystem II excitation in response to rapid environmental change. *Biochimica et Biophysica Acta (BBA)—Bioenergetics*, *1847*(4–5), 468–485. https://doi.org/10.1016/j.bbabio.2015.02.008

De Souza, T. C., De Castro, E. M., Magalhães, P. C., Alves, E. T., & Pereira, F. J. (2012). Early characterization of maize plants in selection cycles under soil flooding. *Plant Breeding*, *131*(4), 493–501. https://doi.org/10.1111/j.1439-0523.2012.01973.x

Ferreira, J. P., Marques, D. M., Karam, D., Borghi, E., Magalhães, P. C., Souza, K. R. D., Arantes, S. D., & Souza, T. C. (2024). How does early defoliation influence the morphophysiology and biochemical characteristics of maize? *Plant Growth Regulation*, *103*, 747–761. https://doi.org/10.1007/s10725-024-01145-x

Freschet, G. T., Cornelissen, J. H. C., van Logtestijn, R. S. P., & Aerts, R. (2010). Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology*, *98*(2), 362–373. https://doi.org/10.1111/j.1365-2745.2009.01615.x

Gao, J., Zhao, Y., Zhao, Z., Liu, W., Jiang, C., Li, J., Zhang, Z., Zhang, H., Zhang, Y., Wang, X., Sun, X., & Li, Z. (2023). RRS1 shapes robust root system to enhance drought resistance in rice. *New Phytologist*, *238*(3), 1146–1162. https://doi.org/10.1111/nph.18775

Guo, Y. Y., Li, H. J., Liu, J., Bai, Y. W., Xue, J. Q., & Zhang, R. H. (2020). Melatonin alleviates drought-induced damage of photosynthetic apparatus in maize seedlings. *Russian Journal of Plant Physiology*, *67*(2), 312–322. https://doi.org/10.1134/S1021443720020053

Iqbal, N., Masood, A., & Khan, N. A. (2012). Analyzing the significance of defoliation in growth, photosynthetic compensation and source-sink relations. *Photosynthetica*, *50*(2), 161–170. https://doi.org/10.1007/s11099-012-0029-3

Jahan, N., Islam, M. R., & Hasan, M. A. (2022). Effect of defoliation on growth and yield of maize. *Bangladesh Agronomy Journal*, *25*(2), 31–41. https://doi.org/10.3329/baj.v25i2.65927

Karam, D., Borghi, E., Magalhaes, P. C., Paes, M. C. D., Pereira Filho, I. A., Mantovani, E. C., Souza, T. C., & Adegas, F. S (2020). *Antecipe cultivo intercalar antecipado Embrapa* (1st ed.). Embrapa.

Keya, S. S., Islam, M. R., Pham, H., Rahman, M. A., Bulle, M., Patwary, A., Kanika, M. M. A. R., Hemel, F. H., Ghosh, T. K., Huda, N., Hawa, Z., Rahman, M. M., & Ravelombola, W. (2025). Thirsty, soaked, and thriving: Maize morpho-physiological and biochemical responses to sequential drought, waterlogging, and re-drying. *Plant Stress*, *15*, 100722. https://doi.org/10.1016/j.stress.2024.100722

Le Stradic, S., Roumet, C., Durigan, G., Cancian, L., & Fidelis, A. (2021). Variation in biomass allocation and root functional parameters in response to fire history in Brazilian savannas. *Journal of Ecology*, *109*(12), 4143–4157. https://doi.org/10.1111/1365-2745.13786

Liu, W.-J., Liu, H., Chen, Y.-E., Yin, Y., Zhang, Z.-W., Song, J., Chang, L.-J., Zhang, F.-L., Wang, D., Dai, X.-H., Wei, C., Xiong, M., Yuan, S., & Zhao, J. (2022). Chloroplastic photoprotective strategies differ between bundle sheath and mesophyll cells in maize (*Zea mays* L.) under drought. *Frontiers in Plant Science*, *13*, 885781. https://doi.org/10.3389/fpls.2022.885781

Liu, Y., Cordero, I., & Bardgett, R. D. (2023). Defoliation and fertilisation differentially moderate root trait effects on soil abiotic and biotic properties. *Journal of Ecology*, *111*, 2733–2749. https://doi.org/10.1111/1365-2745.14215

Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence—A practical guide. *Journal of Experimental Botany*, *51*(345), 659–668. https://doi.org/10.1093/jexbot/51.345.659

Montgomery, E. G. (1911). Correlation studies in corn. *Nebraska Agricultural Experiment Station Annual Report*, *24*, 108–159.

Pearson, A., & Fletcher, A. L. (2009). Effect of total defoliation on maize growth and yield. *Agronomy New Zealand*, *39*, 1–6.

Prasanna, B. M., Cairns, J. E., Zaidi, P. H., Beyene, Y., Makumbi, D., Gowda, M., Magorokosho, C., Zaman-Allah, M., Olsen, M., Das, A., Worku, M., Gethi, J., Vivek, B. S., Nair, S. K., Rashid, Z., Vinayan, M. T., Issa, A. B., San Vicente, F., Dhliwayo, T., & Zhang, X. (2021). Beat the stress: Breeding for climate resilience in maize for the tropical rainfed environments. *Theoretical and Applied Genetics*, *134*, 1729–1752. https://doi.org/10.1007/s00122-021-03773-7

Ryser, P. (1996). The importance of tissue density for growth and life span of leaves and roots: A comparison of five ecologically contrasting grasses. *Functional Ecology*, *10*(6), 717–723. https://doi.org/10.2307/2390506

Salika, R., & Riffat, J. (2021). Abiotic stress responses in maize: A review. *Acta Physiologiae Plantarum*, *43*, Article 130. https://doi.org/10.1007/s11738-021-03296-0

Souza, T. C., Magalhães, P. C., de Castro, E. M., de Albuquerque, P. E. P., & Marabesi, M. A. (2013). The influence of ABA on water relation, photosynthesis parameters, and chlorophyll fluorescence under drought conditions in two maize hybrids with contrasting drought resistance. *Acta Physiologiae Plantarum*, *35*, 515–527. https://doi.org/10.1007/s11738-012-1093-9

United States Department of Agriculture, Foreign Agricultural Service. (2024). *Production data for almonds and corn*. USDA Foreign Agricultural Service. https://www.fas.usda.gov/data/production?commodity=almonds&commodity=corn

Weemstra, M., Mommer, L., Visser, E. J. W., van Ruijven, J., Kuyper, T. W., Mohren, G. M. J., & Sterck, F. J. (2016). Towards a multidimensional root trait framework: A tree root review. *New Phytologist*, *211*(4), 1159–1169. https://doi.org/10.1111/nph.14003

Wu, H.-Y., Qiao, M.-Y., Zhang, Y.-J., Kang, W.-J., Ma, Q.-H., Gao, H.-Y., Zhang, W.-F., & Jiang, C.-D. (2022). Photosynthetic mechanism of maize yield under fluctuating light. *Plant Physiology*, *191*(2), 957–973. https://doi.org/10.1093/plphys/kiac542

Xu, J., Zou, X., Xu, H., Gong, L., Sun, Z., Zhang, L., Niu, S., Feng, L., Han, L., & Wang, R. (2023). Defoliation at seedling stage enhances maize yield by reducing lodging. *Agronomy Journal*, *115*(2), 544–554. https://doi.org/10.1002/agj2.21266

Zhang, X., Kong, Y., Lv, Y., Yao, F., Cao, Y., Shao, X., Geng, Y., Wang, L., & Wang, Y. (2024). Increased topsoil depth required to support increased grain yield production in high-density maize. *Field Crops Research*, *308*, 109282. https://doi.org/10.1016/j.fcr.2024.109282

Zheng, Z., Powell, J. J., Ye, X., Liu, X., Yuan, Z., & Liu, C. (2021). Overcompensation can be an ideal breeding target. *Plant Science Advances*, *11*, 1376. https://doi.org/10.3390/agronomy11071376

Zhu, H., Zhao, J., & Gong, L. (2021). The morphological and chemical properties of fine roots respond to nitrogen addition in a temperate Schrenk's spruce (*Picea schrenkiana*) forest. *Scientific Reports*, *11*, Article 3839. https://doi.org/10.1038/s41598-021-83151-x

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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