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Stage- and Level-Dependent Effects of Simulated Fall Armyworm Defoliation on Maize Growth, Ear Development, and Yield Under Humid Tropical Conditions

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Abstract

Fall armyworm (*Spodoptera frugiperda* J.E. Smith) (Lepidoptera, Noctuidae) is an important pest of maize in Africa, where larval feeding can cause extensive foliar damage and potentially reduce grain yield. However, the relationship between the level and timing of foliar damage and final yield loss is not necessarily proportional. This study evaluated the effect of simulated defoliation at four levels (25, 50, 75, and 100%) imposed at three maize crop growth stages (V3, V8, VT) during two cropping seasons in 2022 (Season 1: March–July; Season 2: September–December), on maize growth, ear development, ear quality, and grain yield under humid tropical conditions of Yaoundé Cameroon using the maize variety ACR06TZLCOMP4C4F2. Thirteen treatments, including twelve defoliation level-crop growth stage combinations plus one undefoliated control, were applied in a randomized complete block design with three replicates. Artificial defoliation was imposed once at the designated crop growth stage by manually removing the corresponding proportion of the leaf blade. Plant height, ear diameter, ear length, ear fill percentage, ear quality, and grain yield were assessed at harvest. Plant height was significantly affected by defoliation level and season, whereas ear diameter, ear length, ear fill percentage, ear quality, and grain yield were more strongly affected by defoliation level and the crop growth stage at which defoliation occurred. At V3, differences in estimated grain yield among defoliation levels were not statistically significant in either season, although the numerical yield responses varied between seasons. In contrast, severe defoliation (≥75%) at V8 and VT substantially reduced ear development and estimated grain yield. In season 1, estimated grain yield declined from 6.1 t ha^{-1} in the undefoliated treatment to 1.2 and 0.8 t ha^{-1} following 100% defoliation at V8 and VT, respectively. In season 2, corresponding estimated yields were 2.2, 0.0, and 0.4 t ha^{-1}. Principal component analysis showed that yield, ear fill percentage, ear diameter, ear quality, and yield loss were closely associated, whereas plant height was primarily associated with a separate principal component. These findings indicate that the effects of simulated defoliation on maize productivity depend on its level, timing, and the environmental conditions of the cropping season. The results characterize biological response of maize to simulated defoliation at different growth stages and highlight the importance of defoliation severity and timing in determining crop performance. Their relevance to practical fall armyworm management requires further validated under natural infestation conditions, across additional environments and maize genotypes, and through studies incorporating economic assessments.

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1. Introduction

Fall armyworm (FAW) *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) is native to tropical and subtropical regions of the Americas [1]. Since its first detection in Africa in 2016 [2], the pest has spread rapidly across the continent and subsequently established in other regions, including India [3] and China [4]. FAW is now considered one of the most important insect pests affecting maize production globally [5]. FAW larvae primarily feed on maize foliage, particularly during the vegetative stages, but may also damage tassels, silks, ears, and developing kernels. Severe feeding can substantially reduce photosynthetically active leaf area, thereby affecting plant growth, reproductive development, and grain production [6–9]. Foliar damage is particularly conspicuous during the whorl stages, where shredded leaves and extensive feeding injury can cause considerable concern among farmers [10]. Damage during early vegetative stages (V1–V9) significantly reduces plant height, stalk thickness, leaf area, and biomass, whereas damage during late vegetative and reproductive stages (V9–R1) increases injury to ears and grains, directly reducing yield because less time remains for recovery and because assimilate demand by reproductive sinks is increasing [6]. Feeding during tasseling interferes with pollen production, and silk damage leads to poor fertilization and reduced grain set [8]. Despite FAW's destructive feeding capacity, leaf injury does not always translate into proportional yield loss [11–13]. Maize can exhibit reduced biomass after defoliation and fully or partially compensate, depending on soil conditions, genetics, cultural practices, and environmental factors [14]. Under optimal conditions, maize can tolerate up to 50% defoliation without yield penalties [8,13]. Compensation involves increased photosynthesis and mobilization of stored resources [15,16] and may be influenced by fertilization practices [14] and varietal differences [14–17]. In Africa, early FAW impact assessments reported large yield losses: 21–52% across 12 countries [18], 22–67% in West Africa [10], and up to 32% in East Africa [19]. Economic losses associated with FAW have also been substantial, although estimates vary among studies and assessment approaches [10,20–23]. Several estimates were based on farmer surveys and community-level assessments rather than direct biophysical measurements [24–26], highlighting uncertainty in extrapolating FAW infestation to actual yield and economic losses. Effective FAW management requires assessment of pest abundance and/or crop damage relative to an economic threshold, with damage ratings commonly used to guide management decisions [27,28]. Because yield loss can vary with the level of crop damage [11,26,28], defining the relationship between defoliation level, crop growth stage, and yield response is important for developing stage-specific management decisions.

Artificial defoliation has been widely used to investigate maize responses to leaf-area loss, although the approaches and objectives have differed among studies. Singh and Nair [29], for example, examined partial and complete leaf removal at different developmental stages and showed that the effects depended on the timing and extent of defoliation. Defoliation at the 16th fully expanded leaf stage reduced leaf area index and several yield components, including ear number, ear length, ear diameter and 1000-grain weight. However, partial leaf removal at the 10th fully expanded leaf stage, intended to modify canopy architecture, sometimes increased yield under high plant density. Similarly, Yao et al. [30] demonstrated that the timing and intensity of defoliation influenced maize growth and reproductive development, with silk growth particularly sensitive to defoliation and early-season damage resulting in substantial yield losses. These findings illustrate that maize

responses to leaf removal are determined not only by defoliation intensity but also by the developmental stage and the plant processes affected.

More recent studies have used artificial defoliation to investigate maize responses to damage associated with fall armyworm (FAW). Blanco et al. [31] examined early-season defoliation and its implications for FAW management thresholds, while Tshiabukole et al. [32] evaluated five levels of leaf-blade removal (0%, 25%, 50%, 75% and 100%) at V3 and VT in two quality protein maize varieties. Tshiabukole et al. [32] therefore provide a particularly relevant comparison for the present study because they used the same defoliation levels at two of the three growth stages considered here. In a different approach, Tashiro et al. [33] simulated FAW-related injury through the removal of expanded leaves, leaf punching and injury to expanding leaves at early maize developmental stages. Their study further demonstrates that simulated FAW damage can be represented through different forms of leaf injury and that the choice of simulation method influences the biological responses being investigated. Collectively, these studies establish that maize compensation following defoliation has already received considerable attention; consequently, the contribution of the present study is not the introduction of artificial defoliation as a method, but the evaluation of a common gradient of leaf-blade removal across three growth stages under humid tropical conditions in Central Africa.

The four defoliation levels used in the present study (25%, 50%, 75% and 100%) represent a progressive gradient of leaf-blade removal, ranging from partial removal to complete removal. This gradient allows the response to increasing severity of leaf-area loss to be examined, including the plant's capacity to compensate following substantial removal of its foliage. These percentages are experimental levels of simulated leaf-blade removal; they should not be interpreted as equivalent categories of FAW infestation or as direct measures of field damage severity. The three growth stages were selected to represent different phases of crop development: V3, an early vegetative stage; V8, an intermediate vegetative stage; and VT, the tasseling stage, marking the transition to reproductive development. Evaluating the same defoliation gradient at these stages allows comparison of maize responses when leaf-area removal occurs at different points in crop development.

It is also important to distinguish this experimental approach from actual FAW injury. FAW larvae do not necessarily remove a uniform proportion of the leaf blade. Their feeding can involve scraping and windowing of leaf tissues, shredding of leaves as they emerge from the whorl, repeated feeding as larvae develops, and, depending on the timing and location of infestation, injury to tassels, silks, ears and developing kernels. In contrast, the present experiment imposed a single, controlled removal of a specified proportion of the leaf blade at each designated growth stage. It therefore isolates the effects of the amount and timing of leaf-blade removal, but does not reproduce the full range, feeding pattern or temporal progression of natural FAW injury. The findings should consequently be interpreted as evidence of maize responses to simulated leaf-area loss rather than as a direct reproduction of all forms of FAW damage.

Despite previous studies on maize defoliation and compensation, information remains limited on how a common gradient of leaf-blade removal affects maize at early vegetative (V3), intermediate vegetative (V8), and tasseling (VT) stages under the warm, humid tropical conditions of Central Africa. In particular, although Tshiabukole et al. [32] evaluated the same five defoliation levels at V3 and VT, their study did not include V8. The present study extends this comparison by incorporating V8, evaluating one improved maize variety over two cropping seasons in Yaoundé, Cameroon, and assessing responses in plant height, ear development, ear fill, ear quality and grain yield. The two-season evaluation also provides an opportunity to examine whether responses to simulated defoliation differ under contrasting seasonal conditions within the same humid tropical environment.

The present study, therefore, evaluated maize responses to different levels of simulated defoliation imposed at V3, V8, and VT over two cropping seasons (Season 1: March–July; Season 2: September–December) under humid tropical conditions in Cameroon. Specifically, we assessed the effects of defoliation level and timing on plant height, ear development, ear fill percentage, ear quality, grain yield, and yield loss. We hypothesized that: (i) increasing defoliation level would progressively reduce maize yield and yield-related traits; (ii) maize would exhibit greater capacity to compensate for defoliation imposed during early vegetative growth than for equivalent defoliation imposed during V8 or VT; and (iii) the magnitude of yield response would differ between cropping seasons because of differences in environmental conditions.

2. Methodology

2.1. Experimental Site

The experiment was conducted at the International Institute of Tropical Agriculture (IITA) research station in Nkolbisson, Yaoundé, Cameroon. The site is located within Cameroon's bimodal humid forest agroecology (03°51.791′ N, 011°27.706′ E; 747 m a.s.l.). The area is characterized by two distinct cropping seasons: the first (season 1) from March to July and the second (season 2) from September to December. Maize was planted on 14 March 2022 in season 1 and on 29 September 2022 in season 2. The experiment was conducted during both seasons of 2022 under rainfed conditions. Seasonal rainfall distribution differed markedly between the two seasons. Season 1 had a longer but less evenly distributed rainfall pattern, whereas season 2 was shorter, with more concentrated rainfall and critically important during the reproductive phase (Figure 1). Figure 1 is provided as a descriptive environmental context for the two cropping seasons and was not used directly in the statistical analyses. Periods where the rainfall curve falls below the temperature curve are generally considered relatively dry periods under the ombrothermic interpretation of climatic data.

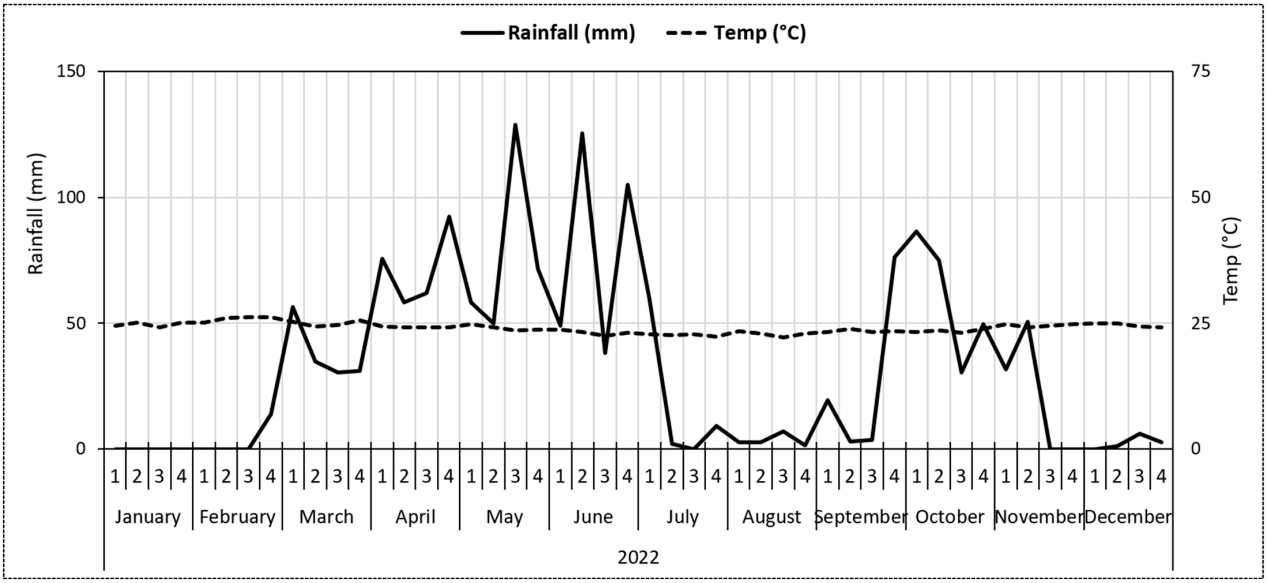


Figure 1. Rainfall and temperature dynamics at the experimental site during the two maize cropping seasons in 2022. Season 1 occurred from March to July and season 2 from September to December. The figure is presented to provide environmental context for the experimental conditions during the study. Meteorological data were obtained from the IITA weather station in Yaoundé, Cameroon (IITA, 2022). Rainfall values represent weekly totals calculated from daily rainfall records (mm), and temperature values represent weekly averages calculated from mean daily temperatures (°C).

2.2. Experimental Design and Treatments

The experiment was conducted at the same research site during both cropping seasons in a randomized complete block design with three blocks serving as replications. Blocks were arranged along a fertility gradient to reduce the potential influence of spatial variation in soil fertility. The use of three replications was determined by the available experimental land and resources. The experiment evaluated simulated defoliation at three crop growth stages: V3 (three fully collared leaves; early vegetative stage), V8 (eight fully collared leaves; mid-vegetative stage), and VT (tasselling, when the final tassel branch was fully visible; flowering; late vegetative stage) [34]. Four levels of artificial defoliation were imposed when plants reached the specified growth stages (V3, V8, and VT) according to the phenological criteria described by Endicott et al. [33], at each stage 25%, 50% 75%, and 100% of the leaf blade. An undefoliated treatment was included as a control.

The 12 defoliation-stage combinations were:

- T1: 25% defoliation at V3;
- T2: 50% defoliation at V3;
- T3: 75% defoliation at V3;
- T4: 100% defoliation at V3;
- T5: 25% defoliation at V8;
- T6: 50% defoliation at V8;
- T7: 75% defoliation at V8;
- T8: 100% defoliation at V8;
- T9: 25% defoliation at VT;
- T10: 50% defoliation at VT;
- T11: 75% defoliation at VT;
- T12: 100% defoliation at VT;
- T13: 0% defoliation (undefoliated control).

The 0% treatment served as a common undefoliated reference treatment for assessing responses to simulated defoliation across all crop growth stages. Because no leaf-area removal was imposed, the control treatment was not stage-specific and was therefore shared across the V3, V8, and VT comparisons.

2.3. Plant Material and Plot Establishment

The maize variety used was ACR06TZLCOMP4C4F2, an improved, high-yielding variety described as tolerant to low soil nitrogen. Maize was planted at a spacing of 0.50 m within and between rows, with three seeds initially planted per hill. Ten days after planting, plants were thinned to two plants per hill. Each experimental plot consisted of 6 hills, with two plants per hill, for a total of 12 plants per plot. Maize was planted at a spacing of 0.50 m within and between rows. The six hills occupied an effective area of 1.5 m^2 (1.0 m × 1.5 m), and all 12 plants within this area were evaluated. This same 1.5 m^2 plot area was used as the sample area for yield estimation and subsequent conversion of kernel number to a hectare basis. To minimize treatment interference, a 1 m alley separated adjacent plots. A border row of maize was established around the experimental area to reduce edge effects. Replicates were also separated by 1 m alleys. The 13 treatments were randomly assigned to plots within each block. Standard agronomic practices recommended for maize production in the study area were followed throughout the experiment. The trials were fertilized twice as side-dressings: first, NPK (20-10-10) at 11 g/plant 2 wk after planting (soon after thinning), and second, urea at 11 g/plant 4 wk after planting (WAP) (after weeding and mounding). Control plants were treated bi-weekly by spraying with the insecticide GREMEC (emamectin benzoate, 300 g/ha at 10 g/sprayer in 15 L of water, Le Grenier du Monde Rural (GMR) SARL, Bafoussam, Cameroon) to keep the plants completely free

of FAW. No insecticides were applied during the experiment to avoid interference with treatment effects.

2.4. Artificial Defoliation Treatments

Defoliation treatments were applied manually at the designated crop growth stages (V3, V8, and VT). Artificial defoliation was applied once to all leaves, not repeatedly. Leaf blades were clipped uniformly across leaves by cutting the specified proportion of the fully expanded leaves using scissors (Figure 2). The length of each leaf was measured to determine the proportion to be removed. Partial defoliation treatments (25%, 50%, and 75%) were imposed by clipping the corresponding proportion of each leaf from its apical end, whereas complete defoliation (100%) involved removing the entire leaf blade. Artificial clipping was chosen to ensure uniform, controlled defoliation levels across treatments, minimizing variability associated with natural fall armyworm infestations and enabling accurate assessment of maize responses to varying damage intensities and crop growth stages. The procedure was applied uniformly to all fully expanded leaves present on the plants at the time of treatment, including older and younger leaves, and consistently across all plants within each treatment plot. Unlike this controlled removal of leaf tissue, natural fall armyworm feeding can produce irregular damage patterns, involve repeated feeding, and affect developing leaves within the whorl and reproductive structures. Thus, the clipping procedure simulated defined levels of leaf-blade removal rather than the full pattern and progression of natural fall armyworm injury. The target defoliation levels were imposed by removing approximately one-quarter (25%), one-half (50%), three-quarters (75%), or the entire leaf blade (100%) from each leaf (Figure 2). Defoliation was imposed consistently across all plants within a treatment plot to achieve the designated level of simulated damage.



Figure 2. Artificial defoliation treatments imposed by manually cutting the leaf blade to achieve 0%, 25%, 50%, 75%, and 100% at the VT growth stage. The photographs were taken from actual experimental plants and illustrate the defoliation levels applied during the study.

2.5. Data Collection

Data were collected from all plants within each experimental plot. Plant height was measured at crop maturity, from the soil surface to the uppermost plant structure, following the experimental measurement procedure. The number of plants and ears harvested in each plot was recorded. Because plants in this experiment produced only one harvestable ear, the number of ears harvested corresponded directly to the number of plants producing harvestable ears. The Harvest rate (%) was therefore calculated as:

$$\text{Harvest rate (\%)} = \frac{\text{Number of ears harvested}}{\text{Number of plants per plot}} \times 100$$

Ear diameter and ear length were measured for harvested ears. Ear diameter and ear length were expressed in centimeters. Ear fill percentage was expressed as the percentage of kernel positions filled on harvested ears. For each ear, the number of kernel rows was recorded. The number of kernels in the longest and shortest rows were also counted, and the average number of kernels per row was calculated.

The average number of kernels per row was multiplied by the number of rows of kernels to estimate the total number of kernels per ear.

Ear appearance was evaluated using a five-point scale from 1 to 5, where 5 = excellent, 4 = very good, 3 = good, 2 = fair, and 1 = poor [35]. Ratings were based on visual characteristics affecting the commercial acceptability of ears, including overall appearance, ear fill, uniformity, and visible damage. The resulting score was used as an appearance-based indicator of ear marketability. This index reflects the potential market acceptance of ears based on visual quality attributes rather than actual consumer preference, commercial grading, or sale price.

At crop maturity, yield components were assessed from all plants in each replicate. For each cob harvested from the sample area, the number of kernel rows was counted. The number of kernels in the longest and shortest rows was also recorded, and the average number of kernels per row was calculated. The average number of kernels per row was multiplied by the number of rows to give the number of kernels per ear. To determine the number of kernels per sampled area, the kernels on each cob were summed.

The number of kernels per hectare was estimated by multiplying the number of kernels counted in the 1.5 m^2 plot by 10,000 m^2 and dividing by 1.5 m^2, which corresponds to the effective area occupied by the 12 evaluated maize plants [12]. To estimate bushels per hectare, the estimated number of kernels per hectare was divided by the bushel factor, defined as 90,000 medium kernels per bushel [12,36]. Maize under drought stress typically contains approximately 110,000 small kernels per bushel, while normal maize has 90,000 medium kernels per bushel, and exceptional maize has 70,000 large kernels per bushel. The kernel size category for this study was determined using a kernel-per-bushel factor key, supported by kernel sample measurements. The observed kernel size corresponded to the medium-kernel category, for which a conversion factor of 90,000 kernels per bushel was adopted [36]. This same conversion factor was applied across all treatments to estimate grain yield. Treatment-specific kernel size and thousand-kernel weight were not measured, and the same kernel-per-bushel conversion factor (90,000 kernels per bushel) was applied across all treatments when estimating yield. The estimated yield in tonnes per hectare was obtained by multiplying the number of bushels per hectare by 25.4/1000, where 1 bushel is equal to 25.4 kg [12,36]. This grain-count approach follows the yield-component method described by Blumenthal and Thompson [36] and previously applied to maize under humid tropical conditions in Cameroon and Central Africa [12]. Grain moisture content was not measured; therefore, yield estimates were not adjusted to a standardized grain moisture basis. Yield loss (%) was calculated separately for each cropping season relative to the corresponding undefoliated control using the equation: where Yc is the grain yield of the undefoliated control within the same season, and Yt is the grain yield of the corresponding defoliation treatment. Negative yield-loss values were retained when the yield of a treatment exceeded that of the corresponding control, thereby preserving the observed apparent yield gains rather than truncating these values at zero.

2.6. Statistical Analysis

The data were analyzed using R (version 4.6.1, released on 24 June 2026; R Foundation for Statistical Computing, The R Foundation for Statistical Computing, c/o Institute for Statistics and Mathematics, Wirtschaftsuniversität Wien, Welthandelsplatz 1, 1020 Vienna,

Austria). A combined factorial analysis was first conducted across the two cropping seasons, and Gaussian linear models were then fitted separately for each season using the lm() function. The six response variables analyzed in the separate-season analyses were plant height, ear diameter, ear length, marketability score, grain yield, and ear-fill proportion. All six responses were analyzed using a Gaussian error distribution with an identity link function. Zero grain-yield observations were retained in the analyses as valid numerical values; no observations were excluded or replaced, and no transformation or arbitrary constant was applied to accommodate zero values. Marketability scores, originally recorded on a five-point ordinal scale, were averaged at the plot level and treated as approximately continuous variables. Similarly, ear-fill percentages were converted to proportions and analyzed as continuous, plot-level responses because the data were plot averages rather than binomial counts. The plot was considered the experimental unit, and plant-level measurements were averaged within each plot before analysis to avoid pseudo-replication.

For the combined factorial analysis, seven response variables were evaluated: grain yield, plant height, ear diameter, ear length, ear-fill percentage, marketability score, and yield loss. The analysis included the 12 defoliation treatment combinations comprising three crop growth stages (V3, V8, and VT) and four defoliation intensities (25%, 50%, 75%, and 100%). Defoliation intensity was treated as a categorical factor. The undefoliated control was excluded from this analysis because it was not assigned to a specific crop growth stage. For each response variable, the combined model included season, replication nested within season, crop growth stage, defoliation intensity, and all two-way and three-way interactions among season, crop growth stage, and defoliation intensity. Season and replication nested within season were included as fixed effects, with no random effects specified. The model was expressed as:

$$Y_{ijkl} = \mu + S_i + B_{j(i)} + CS_k + D_l + (CS \times D)_{kl} + (S \times CS)_{ik} + (S \times D)_{il} + (S \times CS \times D)_{ikl} + \varepsilon_{ijkl}$$

where (Y_{ijkl}) is the plot-level response, (μ) is the overall mean, (S_i) is the fixed effect of season, ($B_{j(i)}$) is the fixed effect of replication nested within season, (CS_k) is the fixed effect of crop growth stage, (D_l) is the fixed effect of defoliation intensity, the subsequent terms represent the corresponding two-way and three-way interactions, and (ε_{ijkl}) is the residual error. Type III analysis of variance (ANOVA), implemented using the Anova() function in the car package, was used to evaluate the significance of the model effects. Sum-to-zero contrasts were specified for the categorical factors. F-statistics, together with their corresponding numerator and residual degrees of freedom, were used to assess statistical significance.

For each response variable, the models included replication (block) and the relevant treatment factor as fixed effects, with replication entered first:

$$(Y_{ij} = \mu + B_i + T_j + \varepsilon_{ij})$$

where (Y_{ij}) is the plot-level response, (μ) is the overall mean, (B_i) is the fixed effect of replication, (T_j) is the fixed effect of the treatment factor, and (ε_{ij}) is the residual error. No random effects were included in the final models.

Two sets of planned comparisons were conducted separately for each season. First, crop growth stages (V3, V8, and VT) were compared separately at each defoliation level (25%, 50%, 75%, and 100%). The undefoliated control was excluded from these comparisons because it was not assigned to a specific crop growth stage. Second, defoliation levels (0%, 25%, 50%, 75%, and 100%) were compared separately within each crop growth stage. Each block contained one undefoliated control plot, which served as the common control for comparisons involving all three crop growth stages within that block. Consequently, the

same block-specific control observations were included in each of the three stage-specific comparisons; they were not treated as independent control observations. Treatment effects were evaluated using sequential analyses of variance (ANOVA). The treatment effect was tested after accounting for replication, using F-statistic and its corresponding numerator and residual degrees of freedom from the fitted linear models. Pairwise comparisons among treatment levels were performed using Tukey-adjusted tests implemented with the glht() function in the multcomp package. The Tukey adjustment controlled the family-wise error rate among pairwise comparisons within each fitted model; it was not applied across the separate models, seasons, or response variables. Treatment differences were expressed as differences between estimated treatment means in the original measurement units, with corresponding 95% confidence intervals, to show the magnitude and uncertainty of the observed effects alongside statistical significance. The estimated pairwise treatment differences, their standard errors, Tukey-adjusted *p*-values, and simultaneous 95% confidence intervals are provided in Supplementary Tables S1–S12. These comparisons used the residual degrees of freedom and t-distribution of the fitted linear models. Statistical significance was set at ($p < 0.05$). Model assumptions diagnostics included the Shapiro–Wilk test of residual normality, normal Q–Q plots, residual-versus-fitted plots. Across the 69 Shapiro–Wilk tests conducted, one indicated a marginal departure from normality for grain yield in season 1 in the comparison among defoliation levels ($W = 0.87879$, $p = 0.04552$). The Gaussian model was retained for this response without transformation. Residual-versus-fitted plots were examined to assess patterns suggestive of non-constant variance. Harvest rate was not subjected to inferential statistical analysis because it was consistently 100% across all treatments and both seasons, resulting in no variation in this response.

Principal Component Analysis (PCA) was conducted separately for each season using standardized plot-level data to explore patterns of association among six agronomic traits: plant height, ear diameter, ear length, ear-fill percentage, ear marketability, and grain yield. Yield loss was excluded because it was mathematically derived from grain yield and therefore did not constitute an independent variable. The PCA was used as an exploratory descriptive analysis to summarize multivariate patterns among the measured traits, rather than to establish causal relationships. Analyses were performed using the FactoMineR package, with graphical outputs generated using factoextra and ggbiplot.

3. Results

3.1. Overall Effects of Defoliation, Crop Growth Stages, and Season on Maize Performance

Several response variables exhibited significant interactions among season, defoliation level, and crop growth stage, indicating that the effects of defoliation depended on the timing of damage and, for some traits, the season in which the experiment was conducted (Table 1).

Table 1. Effects of crop growth stage, defoliation, season, and their interactions on maize traits.

Factors	Plant Height	Ear Diameter	Ear Length	Ear Fill Percentage	Ear Marketability	Yield	Yield Loss
Crop growth stages (CS)	0.462	**0.002** *	**0.007** *	**<0.001** *	**<0.001** *	**<0.001** *	0.028 *
Defoliation (D)	**0.017** *	**<0.001** *	**0.013** *	**<0.001** *	**<0.001** *	**<0.001** *	**<0.001** *
Season (S)	**<0.001** *	**<0.001** *	**<0.001** *	**<0.001** *	**<0.001** *	**<0.001** *	0.389
CS x D	0.160	**0.066**	0.304	**<0.001** *	**<0.001** *	**<0.001** *	**0.006** *
CS x S	0.576	0.468	0.222	0.857	0.015 *	0.124	1.000
D x S	0.720	**0.003** *	**0.029** *	0.200	**<0.001** *	**0.014** *	0.961
CS x D x S	0.432	0.464	0.413	0.501	0.478	0.273	0.449

* Significant effects at $p < 0.05$.

Regarding vegetative growth, defoliation level ($p = 0.017$) and season ($p < 0.001$) significantly affected plant height, whereas the crop growth stage at which defoliation was applied did not ($p = 0.462$). None of the interactions involving defoliation level, crop growth stage, and season were significant for plant height ($p > 0.05$; Table 1).

Analyses of ear size (ear diameter and ear length) showed a significant effect of season ($p < 0.001$ for both), defoliation level ($p = 0.001$ and $p = 0.013$ respectively), and crop growth stage at which defoliation was applied ($p = 0.002$ and $p = 0.007$, respectively, for ear diameter and ear length). For interactions between factors, there were significant interactions between defoliation level and season ($p = 0.003$ and $p = 0.029$ respectively for ear diameter and ear length).

Season, defoliation level, and crop growth stage had a significant effect on ear fill percentage ($p < 0.001$), but only the effect of crop growth stage changed with defoliation level ($p < 0.001$).

Season, defoliation level, and crop growth stage also had significant effects on ear marketability and yield ($p < 0.001$), with significant interaction between defoliation level and season ($p < 0.001$ for marketability; $p = 0.014$ for yield), and between crop growth stage and season ($p = 0.015$ for marketability). Yield loss was affected by the crop growth stage at which defoliation was imposed ($p = 0.028$), the level of defoliation ($p < 0.001$), and the interaction between the two factors ($p = 0.006$) (Table 1).

3.2. Effect of Defoliation on Maize Performance During Different Crop Growth Stages in Two Cropping Seasons in 2022

3.2.1. Plant Height

In season 1, plant height did not differ significantly among defoliation levels at V3, V8, or VT (Table 2). Similarly, crop growth stage did not significantly affect plant height within any defoliation level except at 75% defoliation ($p = 0.033$). In season 2, most comparisons were also not statistically significant. However, at 25% defoliation, plant height differed among crop growth stages ($p = 0.008$; Table 2; Supplementary Tables S1 and S2). The overall seasonal difference in plant height was pronounced, with plants generally taller in season 1 than in season 2. This indicates that seasonal variation between the two cropping seasons contributed substantially to vegetative growth (Table 2).

Table 2. Effect of defoliation levels and crop growth stages on maize plant height (cm) across two cropping seasons.

Season	Defoliation	V3	V8	VT	*F (df = 2, 4)*	*p*
Season 1	0%	207.5 ± 7.3	207.5 ± 7.3	207.5 ± 7.3		
	25%	213.9 ± 10.6	218.1 ± 10.4	235.6 ± 5.3	4.464	0.096
	50%	196.5 ± 12.6	209.2 ± 6.6	215.2 ± 23.1	0.269	0.777
	75%	213.7 ± 8.4 A	188.3 ± 10.2 B	207.8 ± 3.1 AB	9.014	0.033
	100%	198.2 ± 11.1	192.2 ± 20.8	203.0 ± 4.6	0.169	0.850
	F (df = 4, 8)	0.994	1.168	1.465		
	p	0.464	0.393	0.299		
Season 2	0%	177.5 ± 20.4	177.5 ± 20.4	177.5 ± 20.4		
	25%	189.8 ± 7.0 A	190.3 ± 10.0 A	167.7 ± 5.0 B	20.879	0.008
	50%	138.6 ± 10.6	170.1 ± 5.1	167.8 ± 2.2	5.150	0.078
	75%	171.3 ± 5.9	156.3 ± 19.8	186.9 ± 14.9	1.337	0.359
	100%	191.7 ± 6.8	148.0 ± 29.3	152.0 ± 29.6	0.369	0.719
	F (df = 4, 8)	2.849	1.219	0.589		
	p	0.108	0.375	0.680		

Within each defoliation level (row), means followed by the same uppercase letter are not significantly different according to Tukey's HSD test ($p = 0.05$). Pairwise comparisons were performed on plot-level analyses within season. The 0% treatment represents a single common undefoliated control. Control values are repeated across crop growth stages for comparison purposes only and do not represent independent crop-growth-stage-specific control treatments.

3.2.2. Ear Diameter and Length

In season 1, defoliation level significantly affected ear length and ear diameter when defoliation was imposed at the V8 and VT crop growth stages (Table 3). The effect was particularly pronounced for ear diameter at both V8 ($F = 7.625$; df = 4, 8; $p = 0.008$) and VT ($F = 26.132$; df = 4, 8; $p < 0.001$). Ear length was also significantly affected at V8 ($F = 6.863$; df = 4, 8; $p = 0.011$) and VT ($F = 6.400$; df = 4, 8; $p = 0.013$). The effect of crop growth stage was significant only at the 100% defoliation levels on ear diameter ($F = 5.73$; df = 2, 4; $p = 0.041$) and ear length ($F = 7.575$; df = 2, 4; $p = 0.044$; Table 3; Supplementary Tables S3 and S6).

Table 3. Effect of defoliation levels and crop growth stages on maize ear size across two cropping seasons.

Defoliation	Ear Diameter (cm) in Season 1					Ear Length (cm) in Season 1				
	V3	V8	VT	*F (df = 2, 4)*	*p*	V3	V8	VT	*F (df = 2, 4)*	*p*
0%	4.8 ± 0.1	4.8 ± 0.1 a	4.8 ± 0.1 a			24.4 ± 4.5	24.4 ± 4.5 a	24.4 ± 4.5 a		
25%	5.1 ± 0.2	5.0 ± 0.2 a	4.9 ± 0.2 a	2.442	0.203	17.7 ± 0.6	17.6 ± 0.3 ab	18.3 ± 0.8 ab	0.389	0.701
50%	4.8 ± 0.2	4.7 ± 0.1 a	4.6 ± 0.2 a	1.323	0.362	28.0 ± 10.4	17.7 ± 1.9 ab	15.1 ± 0.9 bc	1.487	0.329
75%	4.8 ± 0.2	4.0 ± 0.2 a	4.7 ± 0.1 a	5.509	0.071	16.8 ± 1.0	15.2 ± 0.4 ab	15.4 ± 0.3 bc	1.987	0.252
100%	4.6 ± 0.4 A	2.4 ± 0.7 bB	2.7 ± 0.3 bB	5.728	0.041	17.2 ± 1.2 A	8.4 ± 2.3 bB	8.3 ± 1.2 cB	7.575	0.044
F (df = 4, 8)	0.575	7.625	26.132			1.402	6.863	6.400		
p	0.689	0.008	<0.001			0.316	0.011	0.013		
	Ear diameter (cm) in season 2					Ear length (cm) in season 2				
0%	3.3 ± 0.1	3.3 ± 0.1	3.3 ± 0.1			13.2 ± 0.3	13.2 ± 0.3 a	13.2 ± 0.3		
25%	3.8 ± 0.2	3.4 ± 0.1	3.5 ± 0.5	0.523	0.629	14.2 ± 0.6	12.5 ± 0.7 a	12.6 ± 0.8	1.341	0.358
50%	3.3 ± 0.0	3.2 ± 0.6	3.1 ± 0.2	0.115	0.895	10.5 ± 1.2	11.6 ± 1.8 ab	11.5 ± 0.4	0.061	0.942
75%	3.1 ± 0.1	2.9 ± 0.3	2.9 ± 0.3	0.523	0.639	12.0 ± 1.3	11.3 ± 0.7 ab	11.2 ± 0.4	0.18	0.893
100%	3.5 ± 0.0	2.5 ± 0.5	3.0 ± 0.3	0.793	0.529	14.8 ± 0.6 A	7.8 ± 1.4 bB	11.4 ± 1.7 AB	10.210	0.046
F (df = 4, 8)	3.907	0.746	1.339			3.205	3.414	0.871		
p	0.050	0.587	0.345			0.099	0.043	0.526		

Within each crop growth stage (column), means followed by the same lowercase letter are not significantly different according to Tukey's HSD test ($p = 0.05$). Within each defoliation level (row), means followed by the same uppercase letter are not significantly different according to Tukey's HSD test ($p = 0.05$). Pairwise comparisons were performed on plot-level analyses within season. The 0% treatment represents a single common undefoliated control. Control values are repeated across crop growth stages for comparison purposes only and do not represent independent crop-growth-stage-specific control treatments.

In season 2, however, defoliation level did not significantly affect ear diameter at any crop growth stage, nor was ear diameter significantly influenced by crop growth stage. For ear length, a pattern similar to that observed in season 1 was found at the V8 stage, where defoliation level had a significant effect ($F = 3.414$; df = 4, 8; $p = 0.043$). Similarly, crop growth stage significantly affected ear length only under 100% defoliation ($F = 10.210$; df = 2, 4; $p = 0.046$; Supplementary Tables S3 and S6).

3.2.3. Ear Fill Percentage

In season 1, defoliation level significantly affected ear fill percentage when defoliation occurred at both the V8 and VT crop growth stages (V8: $p = 0.021$; VT: $p < 0.001$; Table 4). Across defoliation levels, the effect of crop growth stage on ear fill percentage was significant only at 100% defoliation ($F = 4.857$; df = 2, 4; $p = 0.046$; Table 4; Supplementary Table S11).

A similar pattern was observed in season 2, with defoliation level significantly affecting ear fill percentage at both V8 ($F = 4.448$; df = 4, 8; $p = 0.025$) and VT ($F = 4.285$; df = 4, 8; $p = 0.038$) stages (Table 4). However, unlike season 1, the effect of crop growth stage on ear fill percentage in season 2 was significant at 75% defoliation ($F = 8.137$ df = 2, 4; $p = 0.039$) and under 100% defoliation ($F = 3.763$; df = 2, 4; $p = 0.040$; Table 4; Supplementary Table S12).

Table 4. Effect of defoliation levels and crop growth stages on ear fill percentage across two seasons.

Ear fill (%) in Season 1					
Defoliation	V3	V8	VT	*F (df = 2, 4)*	*p*
0%	91.7 ± 0.5	91.7 ± 0.5 a	91.7 ± 0.5 ab		
25%	95.0 ± 1.4	91.3 ± 1.9 a	95.3 ± 2.8 a	0.859	0.489
50%	93.8 ± 2.3	92.1 ± 2.7 a	95.4 ± 1.8 a	0.374	0.710
75%	94.1 ± 1.5 A	76.3 ± 5.3 abB	82.0 ± 0.7 bB	6.926	0.050
100%	84.8 ± 9.1 A	39.0 ± 19.5 bAB	28.5 ± 5.4 cB	4.857	0.046
F (df = 4, 8)	0.886	5.422	101.391		
p	0.517	0.021	<0.001		
Ear fill (%) in season 2					
0%	59.4 ± 17.1	59.4 ± 17.1 a	59.4 ± 17.1 a		
25%	58.9 ± 16.3	62.4 ± 9.3 a	56.8 ± 10.6 a	0.108	0.901
50%	31.4 ± 16.6	49.2 ± 10.8 ab	55.8 ± 18.4 a	0.513	0.634
75%	53.3 ± 6.7 A	54.6 ± 17.6 ab A	25.8 ± 12.9 abB	8.137	0.039
100%	55.4 ± 29.0 A	2.5 ± 1.8 bB	6.0 ± 6.0 bB	3.763	0.040
F (df = 4, 8)	0.754	4.448	4.285		
p	0.583	0.025	0.038		

Within each crop growth stage (column), means followed by the same lowercase letter are not significantly different according to Tukey's HSD test ($p = 0.05$). Within each defoliation level (row), means followed by the same uppercase letter are not significantly different according to Tukey's HSD test ($p = 0.05$). Pairwise comparisons were performed on plot-level analyses within the seasons. The 0% treatment represents a single common undefoliated control. Control values are repeated across crop growth stages for comparison purposes only and do not represent independent crop-growth-stage-specific control treatments.

3.2.4. Ear Marketability

In season 1, defoliation level significantly affected mean ear marketability scores when defoliation was imposed at both the V8 and VT crop growth stages ($p < 0.001$ for both stages; Table 5). Across defoliation levels, the effect of crop growth stage on mean ear marketability score was significant only at 100% defoliation (F = 16.010; df = 2, 4; $p = 0.012$; Table 5; Supplementary Table S7).

A similar pattern was observed in season 2, where defoliation level significantly influenced ear marketability at both V8 (F = 4.063; df = 4, 8; $p = 0.033$) and VT (F = 4.303; df = 4, 8; $p = 0.045$) stages (Table 5). Like season 1, crop growth stage significantly affected ear marketability only under 100% defoliation (F = 37.354; df = 2, 4; $p = 0.008$; Table 5; Supplementary Table S8).

Table 5. Effect of defoliation levels and crop growth stages on marketability across two cropping seasons.

Ear Marketability (Scale of 1–5) in Season 1					
Defoliation	V3	V8	VT	*F (df = 2, 4)*	*p*
0%	4.3 ± 0.2	4.3 ± 0.2 a	4.3 ± 0.2 a		
25%	4.3 ± 0.3	4.1 ± 0.3 a	4.4 ± 0.3 a	0.312	0.749
50%	4.6 ± 0.1	3.7 ± 0.3 ab	3.7 ± 0.3 ab	3.278	0.144
75%	4.3 ± 0.4	2.9 ± 0.2 b	2.9 ± 0.1 b	5.802	0.066
100%	4.1 ± 0.5 A	1.4 ± 0.3 cB	1.3 ± 0.2 cB	16.010	0.012
F (df = 4, 8)	0.246	26.420	30.914		
p	0.904	<0.001	<0.001		

Table 5. *Cont.*

Ear Marketability (scale of 1–5) in Season 2					
0%	2.3 ± 0.3	2.3 ± 0.3 a	2.3 ± 0.3 a		
25%	2.2 ± 0.4	2.1 ± 0.3 a	2.1 ± 0.2 a	0.044	0.958
50%	1.4 ± 0.2	1.8 ± 0.3 ab	1.3 ± 0.3 ab	0.469	0.665
75%	1.7 ± 0.2	1.9 ± 0.5 ab	1.6 ± 0.3 ab	0.202	0.828
100%	2.8 ± 0.1 A	0.6 ± 0.2 bB	0.9 ± 0.1 bB	37.354	0.008
F (df = 4, 8)	1.923	4.063	4.303		
p	0.226	0.033	0.045		

Within each crop growth stage (column), means followed by the same lowercase letter are not significantly different according to Tukey's HSD test ($p = 0.05$). Within each defoliation level (row), means followed by the same uppercase letter are not significantly different according to Tukey's HSD test ($p = 0.05$). Pairwise comparisons were performed on plot-level analyses within season. The 0% treatment represents a single common undefoliated control. Control values are repeated across crop growth stages for comparison purposes only and do not represent independent crop-growth-stage-specific control treatments.

3.2.5. Grain Yield and Yield Loss

Grain yield showed a strong response to both defoliation level and crop growth stage (Table 6).

Table 6. Effect of defoliation levels and crop growth stages on maize yield (t ha^{-1}) across two cropping seasons. Under complete defoliation (100%) imposed at V8 during season 2, no harvestable grain was produced, resulting in an estimated yield of zero. This observation reflects complete reproductive failure in the sampled plots under that treatment and should be interpreted within the context of the limited number of experimental replicates.

Season	Defoliation	V3	V8	VT	*F (df = 2, 4)*	*p*
Season 1	0%	6.1 ± 0.7	6.1 ± 0.7 a	6.1 ± 0.7 a		
	25%	5.2 ± 0.5	5.2 ± 0.2 ab	5.8 ± 0.3 a	0.809	0.507
	50%	5.1 ± 0.2	4.9 ± 0.7 ab	4.6 ± 0.5 ab	0.250	0.790
	75%	5.6 ± 0.3 A	3.5 ± 0.6 bB	3.8 ± 0.0 bB	7.579	0.044
	100%	4.8 ± 0.6 A	1.2 ± 0.6 cB	0.8 ± 0.4 cB	11.695	0.021
	F (df = 4, 8)	1.058	8.953	19.593		
	p	0.436	0.005	<0.001		
Season 2	0%	2.2 ± 0.5	2.2 ± 0.5 a	2.2 ± 0.5 a		
	25%	2.9 ± 1.1	3.1 ± 0.4 a	2.1 ± 0.4 a	0.839	0.496
	50%	1.5 ± 0.4	2.0 ± 0.5 ab	1.6 ± 0.6 ab	0.183	0.839
	75%	1.5 ± 0.1	1.6 ± 0.9 ab	1.5 ± 0.5 ab	0.018	0.983
	100%	2.5 ± 0.5 A	0.0 ± 0.0 bB	0.4 ± 0.4 bAB	10.190	0.027
	F (df = 4, 8)	0.827	4.396	2.251		
	p	0.544	0.026	0.036		

Within each crop growth stage (column), means followed by the same lowercase letter are not significantly different according to Tukey's HSD test ($p = 0.05$). Within each defoliation level (row), means followed by the same uppercase letter are not significantly different according to Tukey's HSD test ($p = 0.05$). Pairwise comparisons were performed on plot-level analyses within season. The 0% treatment represents a single common undefoliated control. Control values are repeated across crop growth stages for comparison purposes only and do not represent independent crop-growth-stage-specific control treatments.

In season 1, defoliation level significantly affected yield at both the V8 ($F = 8.953$ df = 4, 8; $p = 0.005$) and VT ($F = 19.593$; df = 4, 8; $p < 0.001$) crop growth stages (Table 6). At V3, grain yield ranged from approximately 5 to 6 t ha^{-1}, and differences among defoliation levels were not statistically significant. not statistically significant. However, given the limited number of plot-level replications, this result should be interpreted as a lack of

statistically detectable differences rather than evidence that defoliation had no biological effect. In contrast, yields at V8 ranged from 1.2 to 6.1 t ha^{-1}, while those at VT ranged from 0.8 to 6.1 t ha^{-1}. At both stages, yield loss increased numerically with defoliation, from approximately 8% at V8 and 5% at VT under lower defoliation to more than 80% at the highest defoliation (Figure 3). The effect of crop growth stage on yield was significant only at 75% (F = 7.579; df = 2, 4; $p = 0.044$) and 100% defoliation (F = 11.695; df = 2, 4; $p = 0.021$; Table 6; Supplementary Table S9).

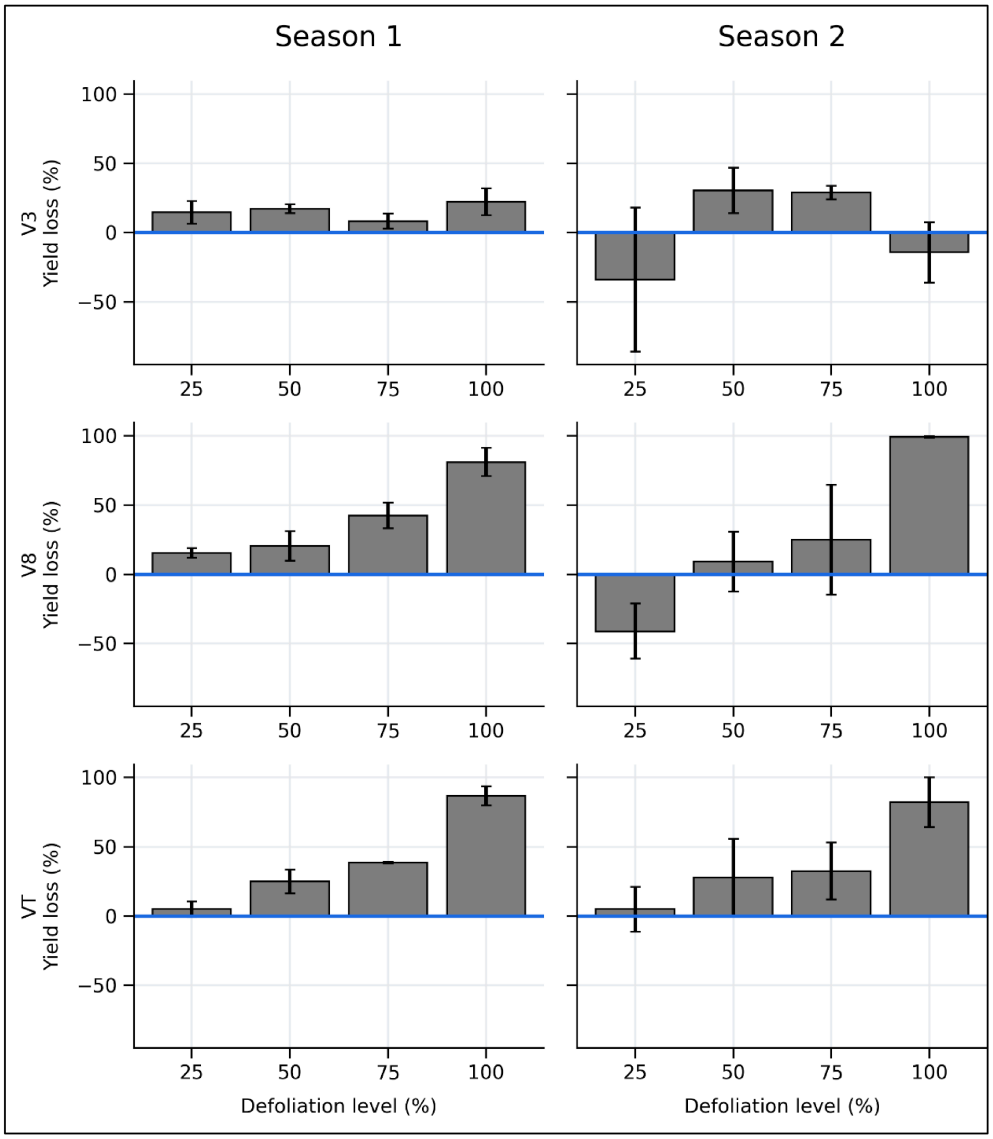


Figure 3. Yield loss (%) associated with simulated defoliation imposed at V3, V8, and VT during two maize cropping seasons (Season 1: March–July and Season 2: September–December). Bars represent mean yield-loss values calculated from three plot-level replicates. Error bars indicate ± standard error (SE). Negative values indicate treatments for which the estimated grain yield exceeded that of the corresponding seasonal undefoliated control.

In season 2, yields were generally lower, ranging from 0.0 to 3.1 t ha^{-1}. Under complete defoliation (100%) at V8, no harvestable grain was produced in the sampled plots, resulting in an estimated grain yield of 0.0 t ha^{-1}. This result reflects severe reproductive failure under complete leaf-area removal and should be interpreted within the context of the limited number of plot replications used in the study. Nevertheless, the effects of defoliation at V8 (F = 4.396; df = 4, 8; $p = 0.026$) and VT (F = 2.251; df = 4, 8; $p = 0.036$) followed a pattern

broadly similar to that observed in season 1 (Table 6). At V3, yield loss remained low under 50% and 75% defoliation, whereas apparent yield gains were observed under 25% and 100% defoliation (Figure 3). At V8 and VT, yield-loss patterns were also generally consistent with those observed in season 1, except for the significant yield gain observed under 25% defoliation at V8. Unlike season 1, where crop growth stage significantly affected yield at 75% and 100% defoliation, this effect in season 2 was significant only at 100% defoliation ($F = 10.190$; df = 2, 4; $p = 0.027$; Table 6; Supplementary Table S10).

3.3. Multivariate Structure of Maize Responses to Defoliation (PCA of Growth and Yield Traits)

3.3.1. Scree Plots of Principal Components Derived from Reproductive and Yield-Related Traits

Principal component analysis was conducted using seven standardized agronomic and yield-related variables: plant height, ear diameter, ear length, ear fill percentage, marketability, and grain yield. The first two principal components explained 85.3% and 81.2% of the total variance in seasons 1 and 2, respectively (Figure 4). Six principal components were obtained for each season; however, only the first five are displayed in the scree plots because the plotting function's default setting limits the display to five components.

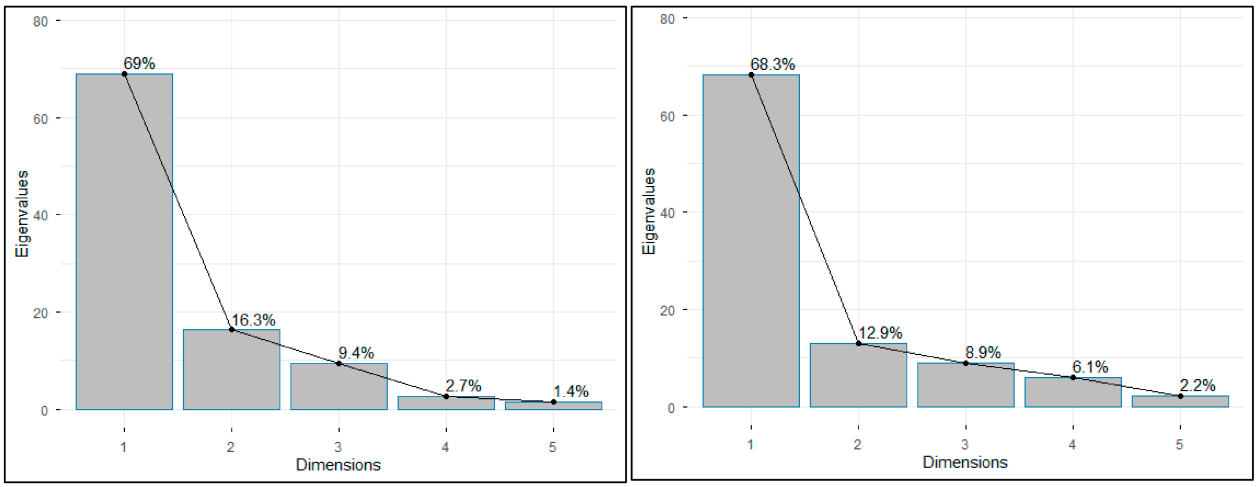
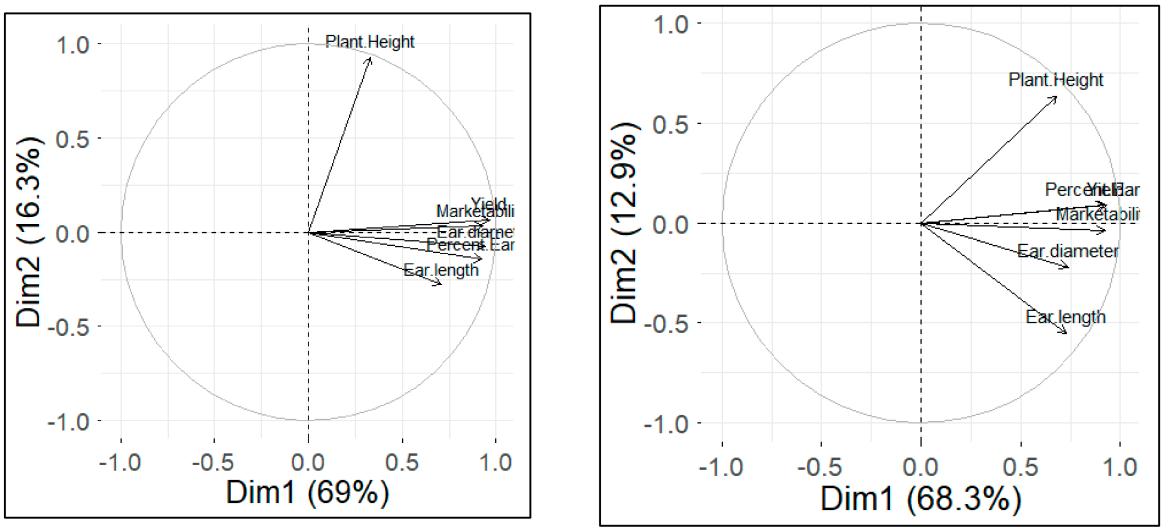


Figure 4. Scree plots from principal component analyses conducted separately for season 1 (**a**) and season 2 (**b**) using plot-level observations. PCA was performed on seven agronomic and yield-related variables (plant height, ear diameter, ear length, ear-fill percentage, marketability, grain yield, and yield loss). Values indicate the percentage of total variance explained by each principal component.

3.3.2. PCA (Biplot) Factor Maps of Reproductive Traits Illustrating Trait Associations and Yield Responses

The PCA provided an exploratory summary of the relationships among vegetative growth, grain yield, and ear-related traits in each cropping seasons (Figure 5). In both seasons, the first two principal components captured the major patterns of variation in the measured traits, with the variable loadings indicating the relative contributions and associations of individual traits to these axes. The clustering of ear-related traits However, because these traits describe related aspects of reproductive performance, their association in the PCA should not be interpreted as independent evidence of distinct biological processes. Similarly, the separation of plant height from some reproductive traits indicates differences in their patterns variation, but does not establish physiological decoupling or a causal compensatory mechanism.

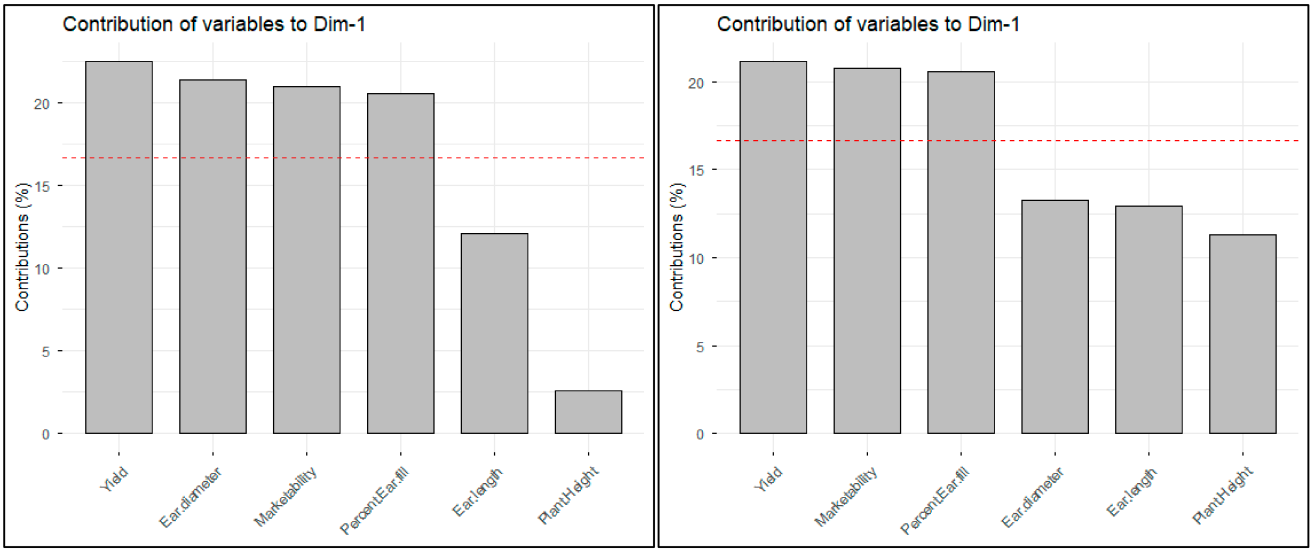


(**a**) (**b**)

Figure 5. Variable factor map from PCA conducted separately for season 1 (**a**) and season 2 (**b**) using plot-level observations, PCA included plant height, ear diameter, ear length, ear-fill percentage, marketability, grain yield, and yield loss. Variables were standardized prior to analysis. The plots illustrate associations among agronomic and yield-related traits across simulated defoliation treatments imposed at V3, V8, and VT.

3.3.3. Drivers of Productivity Under Defoliation (Contributions to Principal Component 1)

The red discontinuous lines represent the average contribution of all variables to dimension 1 (Figure 6a,b). In season 1, yield, ear diameter, marketability, and ear fill percentage were the main contributors to the first principal component (Dimension 1), whereas yield, marketability, and ear fill percentage were the dominant contributors in season 2 (Figure 6a,b). The strong contribution of these reproductive traits to PC1 indicates that variation in reproductive and yield-related traits was an important component of the multivariate structure observed under simulated defoliation.



(**a**) (**b**)

Figure 6. Contributions of the seven standardized variables (plant height, ear diameter, ear length, ear-fill percentage, marketability, grain yield, and yield loss) to principal component 1 (Dimension 1) in season 1 (**a**) and season 2 (**b**). The dashed line indicates the expected average contribution of variables to the principal component.

3.3.4. Contributions of Variables to Principal Component 2 (PC2)

Based on the red discontinuous lines representing the average contribution of all variables to dimension 2, only one variable (plant height) contributed to dimension 2 in season 1, while two variables (plant height and ear length) contributed to dimension 2 in season 2 (Figure 7a,b).

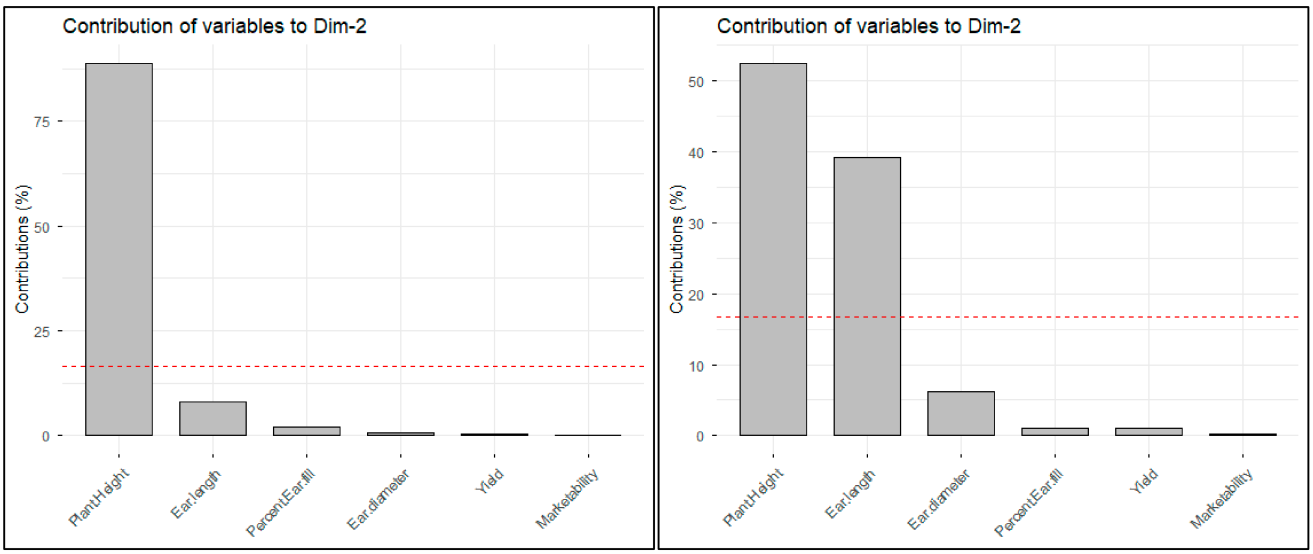


Figure 7. Contributions of the seven standardized variables (plant height, ear diameter, ear length, ear-fill percentage, marketability, grain yield, and yield loss) to principal component 2 (Dimension 2) in season 1 (**a**) and season 2 (**b**). The dashed line indicates the expected average contribution of variables to the principal component.

The PCA therefore separated vegetative growth, represented primarily by plant height, from several reproductive and yield-related variables.

4. Discussion

4.1. Vegetative Response to Defoliation

Defoliation, whether caused by insects or other sources of leaf damage, reduces the photosynthetically active leaf area available to the plant and can consequently affect growth and biomass accumulation. Such damage may lead to reductions in plant height, biomass, and growth rate, as well as alterations in photosynthetic activity [14]. In the present study, plant height was significantly influenced by defoliation level, although seasonal variation appeared to have a stronger effect [37]. Plants were generally taller in season 1 than in season 2, regardless of defoliation level or the crop growth stage at which defoliation was imposed.

The greater plant height observed in season 1 coincided with a longer and more evenly distributed rainfall period, as shown in Figure 1, whereas rainfall in season 2 was shorter and more concentrated. Although rainfall was not quantitatively related to plant height in this study, the contrasting rainfall patterns are consistent with the observed differences in plant growth between seasons and suggest that seasonal differences in rainfall distribution may have contributed to variation in plant development [18]. However, this observation should be interpreted as an association rather than evidence of a direct causal effect of rainfall on plant height.

The effect of defoliation on plant height was most evident at V3 in season 2, where 50% defoliation resulted in significantly shorter plants than those observed under the corresponding treatment in season 1 (138.6 cm versus 177.5 cm; $p = 0.032$). At the other

defoliation levels and crop growth stages, however, differences were not significant. Overall, these findings indicate that both season and defoliation level contributed to variation in plant height, whereas their interaction was not significant. This suggests that the response of plant height to defoliation was broadly consistent across seasons, although the magnitude of plant growth varied.

4.2. Ear Formation and Size (Diameter and Length)

All plants produced ears regardless of season, defoliation level, or crop growth stage at which defoliation was imposed. However, ear diameter, ear length, and ear fill percentage varied with these factors. Thus, defoliation did not prevent ear formation, but severe defoliation, particularly at V8 and VT, compromised subsequent ear development and quality. This distinction between ear formation and the production of marketable ears is important. Under severe defoliation at V8, for example, ear diameter and length were markedly reduced, indicating that ear formation alone did not ensure functional or marketable ears.

Plants defoliated at V3 generally maintained ear size even under high defoliation levels, suggesting greater capacity for recovery during early vegetative growth. In contrast, severe defoliation at V8 and VT substantially reduced ear diameter and length, particularly at complete defoliation. These responses may reflect reduced availability of assimilates for ear development at later crop growth stages; however, assimilate availability was not directly measured in the present study.

Previous studies have shown that ear length is influenced by defoliation timing, intensity, and leaf position [38], consistent with the greater reductions observed at higher defoliation levels and later crop growth stages in the present study. The greater differences among defoliation treatments in season 1 coincided with the contrasting seasonal conditions in the experiment. Because environmental variables other than rainfall were not directly measured, this seasonal pattern should be interpreted as an association rather than evidence of a specific environmental cause. The resulting reductions in ear diameter and length were also associated with lower ear fill percentage, particularly when defoliation exceeded 50% during late vegetative growth (V8) and tasseling (VT).

4.3. Ear-Fill Percentage

According to [37], defoliation can affect, among other parameters, the ear fill percentage. Similar trends were observed for ear fill percentage, marketability of harvested ears, and yield, with PCA results showing that these traits loaded strongly on the first principal component (PC1), indicating a coordinated response of reproductive traits to defoliation stress. Based on ear appearance ratings from 1 to 5, season 1 showed better ear appearance (1.3 to 4.6), compared with 1.3 to 2.8 in season 2, highlighting the influence of season on maize production. These differences coincided with contrasting rainfall distributions between the two cropping seasons (Figure 1). Season 1 extended from March to July, whereas season 2 occurred from September to December. The longer rainfall period in season 1 may have provided more favorable conditions for maize development, consistent with previous reports on maize production under optimal growing conditions [13].

In contrast, rainfall during the second season is generally concentrated between mid-September to mid-November, potentially limiting water availability during reproductive. This period is particularly relevant because maize varieties with a crop cycle of 60–64 days generally reach anthesis within this timeframe []. However, rainfall distribution alone cannot explain the observed seasonal differences, as soil moisture and other potentially influential environmental factors were not systematically measured. Thus, the lower ear-fill percentage and marketability scores observed in season 2 are interpreted as seasonal difference association with contrasting environmental conditions, rather than effects di-

rectly attributed to rainfall. This cautious interpretation is consistent with the recognized sensitivity of maize grain-filling processes to environmental stress [37].

4.4. Marketability of Ears

The observed reduction in ear marketability score at higher defoliation levels, particularly when damage occurred during the late vegetative and reproductive stages, indicated that marketability was more adversely affected as defoliation increased toward reproductive development. In contrast, the lack of a detectable effect following early defoliation at V3 suggests greater compensatory potential during the vegetative phase, when plants can regenerate leaf area and redirect assimilates toward subsequent ear development. This differential response highlights the importance of both the timing and level of defoliation in determining the consequences of leaf damage.

The overall poorer ear quality observed in season 2 coincided with less favorable environmental conditions. However, because environmental variables such as soil moisture were not directly measured, the observed difference should be interpreted as an association rather than evidence of a causal environmental effect. Thus, the effects of leaf damage should not be considered in isolation from the growing environment, particularly during periods critical for reproductive development and grain filling.

The findings are consistent with those of [32], who demonstrated that increasing the level of defoliation during the reproductive phase progressively reduced ear quality. The inclusion of V8 in the present study extends this evidence by showing that maize susceptibility is not restricted to flowering (VT) but may begin during the late vegetative phase. This has important implications for fall armyworm management because protecting the crop before and around the transition to reproductive development may be critical for preventing irreversible effects on ear development and marketable yield.

4.5. Yield of Maize

The relationship between simulated defoliation and yield indicated that the impact of leaf-area removal depended strongly on the crop growth stage at which defoliation occurred. Yield reductions were closely associated with the declines in ear fill percentage and marketability observed at V8 and VT, whereas no statistically significant effect of defoliation level on yield was detected at V3 under the conditions of this experiment. These results are consistent with a greater tolerance of early-season leaf-area removal than of equivalent defoliation imposed during later crop growth stages.

Grain yield differed substantially between the two cropping seasons, indicating that the responses observed under defoliation were influenced by the seasonal growing conditions. Although the rainfall patterns differed between seasons (Figure 1), the experiment was not designed to isolate the effects of individual environmental variables on grain yield. Factors such as soil moisture availability, solar radiation, nutrient dynamics, and other biotic or abiotic stresses were not systematically measured. Consequently, the seasonal differences in yield cannot be attributed specifically to rainfall or temperature. Rather, they reflect the combined influence of environmental conditions associated with each cropping season, together with the responses to the imposed defoliation treatments.

The numerical decline in yield across increasing defoliation levels at V8 and VT is consistent with [39], who identified 50% defoliation as a critical level for maize. However, the present findings suggest that such a threshold should not be considered independently of crop growth stage, as the consequences of defoliation were most evident at V8 and VT rather than at V3. Moreover, the lack of clear statistical separation among some of the higher defoliation levels suggests that the relationship between the extent of leaf damage and yield loss may not be strictly proportional.

The relatively stable yield following V3 defoliation indicates tolerance to moderate early-season leaf loss under the conditions of this study. Moderate leaf loss may be buffered through processes such as assimilate partitioning, increased photosynthetic activity of remaining leaves, and mobilization of stored non-structural carbohydrates from stems and roots, as reported in previous studies [15,16]. However, these mechanisms were not directly measured in the present study. Such mechanisms can help maintain reproductive development despite partial loss of photosynthetic tissue and may explain why moderate defoliation does not necessarily result in proportional yield losses. Similar patterns of yield maintenance following moderate defoliation have been reported in maize under favorable growing conditions exposed to moderate fall armyworm injury or equivalent levels of defoliation [15,16]. The results are consistent with previous studies reporting that maize can maintain productivity following moderate defoliation through compensatory physiological responses [8,15,16,40,41]. In the present study, 25–50% defoliation at V3 did not significantly reduce ear size, ear fill percentage, or yield, supporting the possibility that maize can partially compensate for early-season leaf loss under favorable growing conditions. Because these physiological mechanisms were not directly measured, their role should be considered a biologically plausible explanation rather than a demonstrated response. The apparent yield gains recorded under some defoliation treatments in season 2 should also be interpreted cautiously. These increases were numerical rather than evidence of a consistent yield-enhancing effect of defoliation. In particular, yield differences at V3 were not statistically significant, while the apparent gain under 25% defoliation at V8 was not significantly different from the undefoliated control in the pairwise comparison. Given the three plot-level replications per treatment, some of these differences may reflect experimental variability among plots rather than a biological stimulation of yield by defoliation. Furthermore, grain yield was estimated using a common kernel-per-bushel conversion factor, without determining treatment-specific kernel weight. Consequently, the apparent gains should not be interpreted as evidence that defoliation increased maize productivity.

4.6. Possible Compensatory Mechanisms in Maize: Integrating PCA Evidence and Yield Responses

Crop physiological responses to defoliation may involve redistribution of assimilates from vegetative tissues toward reproductive sinks, particularly when environmental conditions favor resource mobilization [15,16,42]. In maize, such reallocation may help maintain kernel set and grain filling when damage occurs before or around the onset of reproductive development [38,43]. The stability of reproductive traits following early defoliation in this study is consistent with a degree of tolerance to leaf-area removal and may reflect compensatory responses that helped maintain reproductive performance. The PCA results were also consistent with this interpretation, showing that reproductive and yield-related traits contributed differently to the observed patterns of variation than vegetative traits.

4.6.1. Trait Contributions, Drivers of Compensation, and Biological Meaning of Vegetative–Reproductive Decoupling

The PCA separated vegetative and reproductive responses, with yield, ear fill percentage, ear size, and marketability loading strongly on PC1, while plant height was primarily associated with PC2. This pattern suggested that vegetative and reproductive traits contributed differently to the observed variation among treatments under defoliation stress. Consequently, reductions in vegetative growth were not always accompanied by proportional reductions in yield, indicating that reproductive traits and yield responses varied independently across some treatments [14,17].

4.6.2. Compensatory Responses Across Crop Growth Stages

The stage-specific responses further supported this interpretation. At V3, no statistically significant effect of defoliation levels on yield was detected despite variation in vegetative traits, indicating tolerance to early-season leaf-area loss under the conditions of the experiment. In contrast, at V8 and VT, severe defoliation (≥75%) was associated with declines in ear fill percentage, marketability, and yield, which may reflect a reduced capacity for recovery as plants approached reproductive maturity. At these stages, the shorter time available for leaf-area recovery and the increasing demand of reproductive sinks may have limited the ability of plants to tolerate extensive tissue loss [38,43].

4.6.3. Non-Linear Damage–Yield Relationship

The combined PCA and univariate results indicated that the relationship between defoliation and yield was not simply proportional to the amount of leaf area removed. Rather, yield response appeared to depend on the extent to which defoliation disrupts reproductive development. As long as reproductive traits remain relatively coordinated, yield can be buffered despite moderate vegetative damage. Under severe or late-stage defoliation, however, reductions in ear development and marketability are accompanied by substantial yield losses. This interpretation is consistent with previous studies showing that maize can tolerate moderate FAW damage without significant yield penalties under favorable growing conditions [8,11,44]. Similarly, Ref. [11] reported that intermediate levels of FAW damage may have limited effects on yield, while Ref. [39] identified 50% defoliation as a critical level associated with yield reduction.

4.6.4. Practical Implications for Yield Assessment and IPM

These findings suggested that visible leaf damage and vegetative traits such as plant height alone may be insufficient indicators of potential economic loss. Reproductive traits, particularly ear fill percentage, ear size, and marketability, may provide more informative indicators of productivity under defoliation stress. The results also indicated that moderate defoliation, particularly during early vegetative growth, could be tolerated without substantial yield penalties under favorable production conditions. In contrast, severe defoliation at V8 and VT warrants greater attention because the capacity to tolerate leaf-area loss may be lower as plants approach and enter reproductive development.

From an IPM perspective, theresults indicate that the effects of foliar damage on maize productivity depend on both defoliation severity and crop growth stage. However, because the present experiment used simulated defoliation rather than natural FAW infestation, the findings cannot establish larval-density or damage thresholds for insecticide intervention. They should therefore be interpreted as evidence of the biological responses of maize to leaf-area removal under the conditions of this study, rather than as direct management recommendations. Establishing practical stage-specific decision thresholds will require field validation under natural FAW infestation, together with assessments of larval density, infestation patterns, crop response, and the economic costs and benefits of intervention.

4.6.5. Study Limitations and Future Research

Several limitations should be considered when interpreting these findings.

The experiment used three plot-level replications per treatment, which limits the statistical power to detect relatively small treatment effects. Future experiments should consider greater replication where feasible to improve precision and the ability to detect biologically meaningful differences.

Artificial clipping does not reproduce all characteristics of natural FAW feeding. Natural infestations can involve repeated feeding, heterogeneous damage distribution, preferen-

tial feeding on developing leaves, and damage to plant structures other than mature leaf blades, including whorl tissues, tassels, silks, ears, and developing kernels. Accordingly, the simulated defoliation treatments should be interpreted as controlled estimates of maize responses to defined levels of leaf-area removal rather than direct representations of natural FAW infestation. Therefore, the damage levels observed in this experiment should not be directly interpreted as operational FAW action thresholds without validation under natural infestation conditions.

The scope of these findings is also limited by the evaluation of a single maize genotype at one location. Although the experiment covered two cropping seasons, both were conducted at the same location and therefore do not establish the consistency of the observed responses across different environments. Furthermore, other maize genotypes may differ in their tolerance to defoliation and compensatory capacity. Consequently, the findings should be interpreted within the context of the genotype and environmental conditions evaluated in this study and should not be generalized directly to other maize varieties or production environments.

The experiment was conducted at a single location during two cropping seasons. Although the two seasons provided contrasting environmental conditions, additional locations and agroecological zones are needed to determine the broader applicability of the findings. Furthermore, although the experiment covered two contrasting cropping seasons, it was conducted at one location within a single year. Seasonal effects therefore cannot be separated from other environmental influences that may have differed between the two experimental periods. The absence of systematic measurements of soil moisture, solar radiation, and other potentially influential environmental variables also limits the identification of the specific factors responsible for the observed seasonal differences. Further evaluations across multiple years and environments, accompanied by more comprehensive environmental monitoring, would be necessary to establish the consistency and environmental determinants of these responses.

Physiological mechanisms underlying compensation, such as photosynthetic activity, leaf-area recovery, carbohydrate mobilization, and assimilate partitioning, were not directly measured. Grain yield in the present study was estimated using the grain-count method rather than by direct weighing of harvested grain. This approach follows the yield-component method of Blumenthal and Thompson [36] and has previously been applied under the humid tropical conditions of Yaounde, Cameroon [12]. A comparison of grain-count and grain-weight methods under comparable experimental conditions found no significant differences between the two approaches, supporting the use of the grain-count method for field-based yield assessment [ ]. In the present study, the observed kernel size corresponded to the medium-kernel category, supporting the selection of 90,000 kernels per bushel as the common conversion factor. Nevertheless, treatment-specific kernel size and thousand-kernel weight were not measured. This limitation is relevant because defoliation may affect kernel development and grain filling, potentially resulting in differences in kernel weight among treatments that are not captured by a common conversion factor, except that grain filling was measured. Consequently, the estimated yield differences may not fully reflect treatment-related variation in kernel weight. Furthermore, grain moisture content was not measured, and yields were not corrected to a standardized moisture basis. Therefore, the yield values should be interpreted as grain-count-based estimates rather than direct measurements of harvested grain mass. Despite these limitations, the method detected significant reductions in estimated grain yield as defoliation increased at V8 and VT, indicating substantial treatment effects under the conditions evaluated. Future studies should combine kernel counts with direct grain weighing, treatment-specific kernel-weight measurements, and moisture correction to improve the precision of yield assessment. Ex-

periments should integrate controlled defoliation, natural FAW infestations, larval density assessments, corresponding levels of leaf damage, and economic analyses to develop and validate practical stage-specific decision rules.

An important consideration when interpreting these findings is the use of three plot-level replications per treatment. Although the experimental design enabled comparisons of defoliation intensity and timing across two cropping seasons, the relatively small number of replicates limited the precision of some treatment estimates, as reflected in the confidence intervals around pairwise differences. Consequently, nonsignificant comparisons should not be interpreted as evidence that treatments had no biological effect. Rather, they indicate that the observed differences could not be distinguished statistically at the specified significance level under the experimental conditions. The estimated differences and their confidence intervals therefore provide important complementary information for interpreting the magnitude and uncertainty of treatment responses. Further experiments with greater replication would help improve the precision of these estimates and clarify responses where uncertainty remains substantial.

The PCA should be interpreted cautiously because it was based on a relatively small number of plot-level observations in each season. Although it provides a useful descriptive summary of associations among the measured traits, the component structure and variable loadings may be sensitive to the observations included in the analysis. Furthermore, several reproductive variables represent related aspects of crop performance, which may contribute to their association within the same principal component. Consequently, the PCA is considered exploratory and complementary to the univariate analyses, rather than independent confirmation of the biological mechanisms underlying the observed responses.

5. Conclusions

This study demonstrates that moderate simulated defoliation imposed at the V3 stage was not associated with a statistically detectable reduction in grain yield under the conditions evaluated. However, this finding should not be interpreted as evidence that moderate defoliation has no biological effect, particularly given the limited number of plot-level replications. In contrast, severe defoliation (≥75%) during the late vegetative (V8) and tasseling (VT) stages substantially compromised ear development, ear fill percentage, marketability, and yield. The PCA results indicate that reproductive traits were more closely associated with yield than vegetative growth traits and are consistent with the observation that moderate simulated defoliation was not associated with a statistically significant reduction in grain yield under the conditions evaluated.

Under the environmental conditions of season 1, up to 50% defoliation at V3 was not associated with a significant yield reduction. This observation indicates that moderate early-season leaf-area removal may have limited effects on maize productivity under certain growing conditions. However, the responses differed between seasons, emphasizing that the effects of defoliation should be interpreted within the environmental conditions under which the experiment was conducted. Overall, the demonstrate that the biological consequences of simulated defoliation depend on both its severity and the growth stage at which it occurs. Severe defoliation at V8–VT was associated with greater impairment of reproductive traits and yield than moderate early-season defoliation. These results characterize maize responses to leaf-area removal under the tested conditions but do not establish practical FAW management or insecticide intervention thresholds.

Future studies involving natural FAW infestation, additional maize genotypes and contrasting agroecological environments, together with assessments of larval density and the economic costs and benefits of management interventions, are required before practical stage-specific recommendations can be developed.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/plants15233656/s1. Supplementary Table S1. Plant height: Season 1 Estimated differences in cm; Tukey-adjusted pairwise comparisons. Supplementary Table S2. Plant height: Season 2 Estimated differences in cm; Tukey-adjusted pairwise comparisons. Supplementary Table S3. Ear diameter: Season 1 Estimated differences in cm; Tukey-adjusted pairwise comparisons. Supplementary Table S4. Ear diameter: Season 2 Estimated differences in cm; Tukey-adjusted pairwise comparisons. Supplementary Table S5. Ear length: Season 1 Estimated differences in cm; Tukey-adjusted pairwise comparisons. Supplementary Table S6. Ear length: Season 2 Estimated differences in cm; Tukey-adjusted pairwise comparisons. Supplementary Table S7. Ear marketability score: Season 1 Estimated differences in score (1–5); Tukey-adjusted pairwise comparisons. Supplementary Table S8. Ear marketability score: Season 2 Estimated differences in score (1–5); Tukey-adjusted pairwise comparisons. Supplementary Table S9. Grain yield: Season 1 Estimated differences in t ha^{-1}; Tukey-adjusted pairwise comparisons. Supplementary Table S10. Grain yield: Season 2 Estimated differences in t ha^{-1}; Tukey-adjusted pairwise comparisons. Supplementary Table S11. Ear fill: Season 1 Estimated differences in proportion (0–1); Tukey-adjusted pairwise comparisons. Supplementary Table S12. Ear fill: Season 2 Estimated differences in proportion (0–1); Tukey-adjusted pairwise comparisons.

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