

Microclimate diversity across sweet corn varieties and implications for agrobiodiversity in precision intercropping

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Abstract. Pantouw CF, Patandean B, Ritonga AW, Chozin MA, Rachmat A. 2025. Microclimate diversity across sweet corn varieties and implications for agrobiodiversity in precision intercropping. *Biodiversitas* 26: 5238-5247. The intercropping of sweet corn (*Zea mays*) and bird's eye chili (*Capsicum frutescens*) is a promising land-use intensification strategy to improve resource-use efficiency while strengthening agrobiodiversity. This study evaluated four sweet corn varieties (Arinta, Exotic, Talenta, and Paragon) combined with two chili genotypes, Bonita (shade-loving) and Ori 212 (shade-tolerant), arranged in a Randomized Complete Block Design (RCBD) with four replications at the Pasir Kuda Experimental Station, Institut Pertanian Bogor, Bogor, Indonesia. Microclimate parameters (temperature, relative humidity, light intensity) were recorded with data loggers and lux meters, while chili morphophysiological traits included plant height, stem diameter, leaf area, and physiological responses. Results indicated that variation in sweet corn canopy architecture significantly altered microclimatic conditions. Exotic and Talenta reduced light intensity by 43% (to 35,000 lux), which favored the growth of Ori 212 (height 65.25 cm; leaf area 19.61 cm²). Paragon created the coolest and most humid microclimate (29.7°C; 61.95% RH), stimulating maximum leaf expansion in Bonita (20.98 cm²). Arinta maintained higher light levels (47,633 lux), while the open control (>62,000 lux) suppressed chili growth (height 25 cm; leaf area 6-9 cm²) due to heat stress and photoinhibition. Pearson correlation further revealed strong positive associations among photosynthesis, stomatal conductance, and transpiration, demonstrating that microclimate directly regulates chili physiological dynamics. In conclusion, sweet corn canopy diversity plays a decisive role in shaping niche differentiation for chili in intercropping systems. The Exotic-Ori 212 and Paragon-Bonita combinations emerged as the most compatible patterns for achieving balanced growth, photosynthetic efficiency, and strengthened agrobiodiversity in sustainable tropical farming systems.

Keywords: Canopy microclimate, ecophysiological niche, photosynthetic plasticity, shade adaptation, sustainable intensification

INTRODUCTION

Intercropping is an agricultural practice in which two or more crop species are grown simultaneously on the same plot of land (Li et al. 2023). This system has long been adopted by farmers to improve the efficiency of resource use, particularly solar radiation, water, and soil nutrients while also reducing weed competition, suppressing pest and disease incidence, and minimizing the risk of crop failure under climatic fluctuations (Khanal et al. 2021). Within the framework of sustainable agriculture, intercropping functions as a land intensification strategy that enhances total productivity while maintaining ecological balance in agroecosystems (Lan et al. 2023; Wang et al. 2023). The success of such systems largely depends on the compatibility of crop combinations, particularly those that differ in morphological traits, growth requirements, and developmental cycles, so that they complement one another and optimize spatial and temporal resource use (Van Der Werf et al. 2020; Peng et al. 2021).

Light distribution and interspecific interactions are central to the design of intercropping systems. For

example, combining tall and short crop species allows for more uniform light interception across canopy layers, enabling the understory crop to maintain efficient photosynthesis despite partial shading (Bechem et al. 2018; Chen et al. 2024). Conversely, excessive shading may reduce growth, yield, and quality in shade-sensitive horticultural crops when light levels exceed their tolerance thresholds (Zubay et al. 2021; Deng et al. 2022). Thus, technical considerations such as variety selection, planting density, and crop proportion are critical in precision intercropping design.

Sweet corn (*Zea mays* L. *saccharata*) and bird's eye chili (*Capsicum frutescens* L.) are high-value horticultural commodities with significant economic importance and strong market prospects (Ruswandi et al. 2020; Xiang et al. 2021). Sweet corn is preferred by consumers for its sweetness, tender kernels, and relatively short harvest period (Revilla et al. 2021), while bird's eye chili remains a staple commodity with consistently high year-round demand (Widyaningsih et al. 2021). Their combination in intercropping systems offers synergistic potential: sweet corn, as a tall crop, can provide partial shading to alleviate

heat stress in chili, while chili efficiently utilizes inter-row spaces otherwise unexploited by corn (Arta et al. 2024; Patandean et al. 2025). Previous studies on cereal-vegetable intercropping, such as maize-pepper and maize-tomato, have shown improvements in land-use efficiency, microclimate stability, and overall resilience (Chen et al. 2024; Legba et al. 2025). From a practical perspective, both sweet corn and bird's eye chili are high-value commodities with strong market demand in Southeast Asia, making their integration not only ecologically compatible but also economically relevant for smallholder farmers. This dual ecological economic rationale underpins the selection of sweet corn-chili intercropping as the focus of the present study.

Variety selection plays a decisive role in this context (Moore et al. 2022). Differences in canopy architecture, plant height, and leaf density among sweet corn varieties generate variations in light intensity available to the understory crop (Patandean et al. 2025). A previous evaluation of ten sweet corn genotypes, including four commercial hybrids and six hybrids developed by Institut Pertanian Bogor, identified four superior varieties, Arinta, Exotic, Talenta, and Paragon, as representative of contrasting canopy morphologies and yield potential (Patandean et al. 2025). On the other hand, Siahaan et al. (2023) evaluated the shade tolerance of 20 bird's eye chili genotypes and classified them into shade-sensitive, moderately tolerant, shade-tolerant, and shade-loving groups, highlighting significant variation in adaptive strategies.

Although several studies have addressed sweet corn canopy diversity and chili shade tolerance separately, no comprehensive research has directly linked these aspects to evaluate how corn-induced microclimates influence chili adaptation. This gap restricts the formulation of evidence-based recommendations for designing compatible corn-chili intercropping systems that optimize both productivity and agrobiodiversity.

To address this gap, the present study evaluated four sweet corn varieties (Arinta, Exotic, Talenta, and Paragon) and two bird's eye chili genotypes with contrasting shade preferences (Bonita-shade-loving; Ori 212-shade-tolerant). Specifically, the objectives were to: (i) assess how the canopy architecture of sweet corn shapes microclimatic conditions (temperature, relative humidity, and light intensity); (ii) analyze the morphological, phenological, and physiological responses of bird's eye chili under those conditions; and (iii) determine the implications for precision intercropping systems and the enhancement of agrobiodiversity.

MATERIALS AND METHODS

Genetic materials and field conditions

The genetic materials used in this study comprised four previously selected hybrid sweet corn varieties (Patandean et al. 2025) (Table 1) and two bird's eye chili genotypes, one shade-loving and the other shade-tolerant (Siahaan et al. 2023) (Table 2). The field experiment was conducted from August 2024 to February 2025 at the Pasir Kuda Experimental Station (6°36'31.7" S, 106°47'3.26" E),

located within Institut Pertanian Bogor, Bogor, Indonesia. A single-factor Randomized Complete Block Design (RCBD) with four replications (blocks) was used. The single experimental factor was sweet corn variety, consisting of four levels: Arinta, Exotic, Talenta, and Paragon. Each 4 m² plot represented one replicate for a given variety within each block.

Each sweet corn variety was intercropped with two fixed bird's eye chili genotypes (Bonita and Ori 212), which were treated as associated intercrops rather than as independent experimental factors. The purpose of this arrangement was to evaluate how differences in sweet corn canopy architecture influence the microclimatic conditions and the morphophysiological responses of chili plants grown underneath.

Within every plot, five corn plants and five chili plants were randomly selected as sample plants for morphological and physiological observations. Data from these five plants were averaged to obtain the plot mean, which served as the unit of replication for statistical analysis ($n = 4$ per variety). The total experimental area was 384 m², with each raised bed assigned to one corn variety and subdivided into four replicated plots.

Procedures

The experiment was conducted using six raised beds, each measuring 1 m × 32 m. Four beds were allocated to four sweet corn varieties (Arinta, Exotic, Talenta, and Paragon) (Figure 1.A), while the remaining two beds were assigned to monoculture plots of two bird's eye chili genotypes (Bonita and Ori 212) (Figure 1.B).

Each raised bed was divided into four plots measuring 4 m × 1 m (4 m²), representing four replications for each variety. In total, there were 16 intercropped plots (4 corn varieties × 4 replications) and 8 monoculture plots (2 chili genotypes × 4 replications).

In each intercropping bed, one sweet corn variety was combined with the two bird's eye chili genotypes (Bonita and Ori 212), and this pattern was repeated four times along the bed, resulting in a total bed length of 32 m. The spacing between beds was maintained at 80 cm to facilitate irrigation, fertilization, weeding, and pest control. Before planting, basal fertilization was applied at a rate of 1 ton ha⁻¹ of farmyard manure and 2 tons ha⁻¹ of dolomite.

Table 1. List of sweet corn genotypes in Indonesia

Code no.	Genotype	Owner agency
J1	Arinta	Hybrid lines (Faculty of Agriculture, Institut Pertanian Bogor, Bogor)
J2	Exotic	Hybrid commercial variety (Agri Makmur Pertiwi Company, Kediri District, East Java)
J3	Talenta	Hybrid commercial variety (Agri Makmur Pertiwi Company)
J4	Paragon	Hybrid commercial variety (Agri Makmur Pertiwi Company)

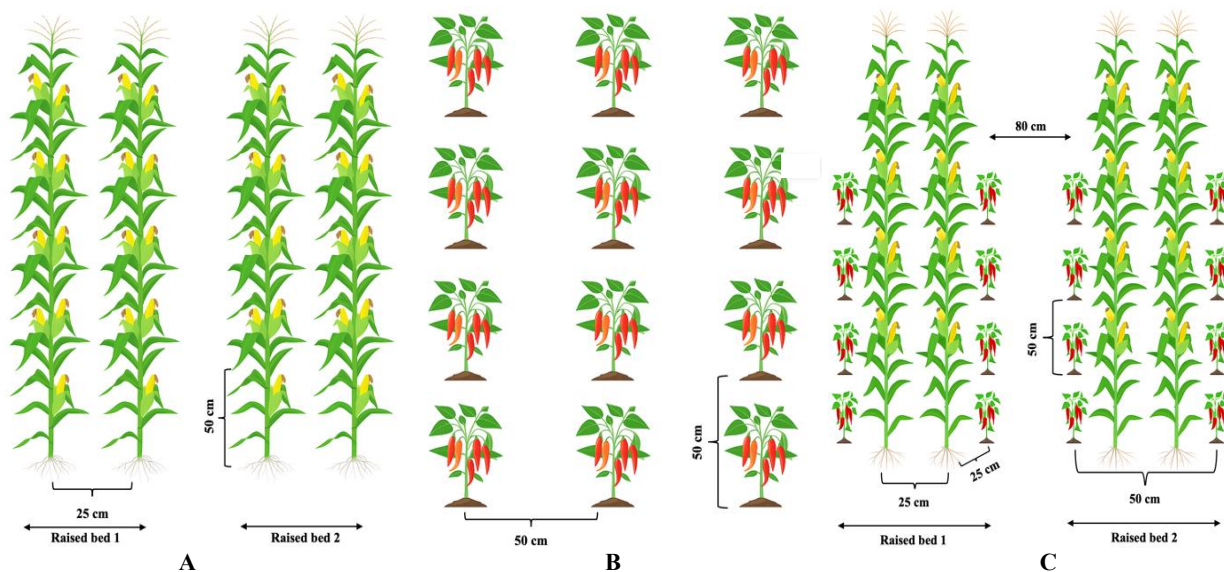


Figure 1. Spatial arrangement of plants in the sweet corn-bird's eye chili intercropping system. A. Planting distance of sweet corn in the intercropping system, B. Planting distance of bird's eye chili in both intercropping and monoculture systems, C. Intercropping layout between sweet corn and chili plants

Table 2. List of bird's eye chili genotypes in Indonesia

Code no.	Genotype	Owner agency	Shading preference
C1	Bonita	Breeding Laboratory, Institut Pertanian Bogor, Bogor	Shade-loving
C2	Ori 212	CV. Aura Seed Indonesia, Kediri District, East Java	Shade-tolerant

Sweet corn was planted at a spacing of 50 cm × 25 cm (50 cm between rows and 25 cm within rows), whereas bird's eye chili was planted at 50 cm × 50 cm (Figure 1.C). Each replicate consisted of 40 sweet corn plants (20 on the left side and 20 on the right side) intercropped with 40 chili plants (20 on each side). Thus, in one intercropping bed comprising four replicates, the total population reached 320 sweet corn plants and 320 chili plants per genotype. This layout ensured uniform plant density and allowed for accurate assessment of microclimatic variations across different canopy structures.

Crop management practices were uniformly applied across all treatments. Irrigation was applied every two days in the absence of rainfall, manual weeding was performed up to three times before harvest, and fertilization was carried out using 300 kg ha⁻¹ of nitrogen, phosphorus and potassium fertilizer. In addition, fungicides and insecticides were applied when necessary, depending on the incidence and severity of pest and disease outbreaks.

Observation of microclimate

Microclimatic conditions were monitored using an Elitech RC-4HC Data Logger to record air temperature (°C) and relative humidity (%) within each raised bed. The device was positioned beneath the corn canopy at

approximately 30 cm above the soil surface, corresponding to the middle layer of the chili canopy. Light intensity (lux) was measured manually using a Digital Lux Meter (LX1010B), which was also positioned beneath the canopy at the same height.

Measurements were conducted at 7-day intervals, beginning at 5 weeks after planting (WAP), and were taken at three fixed times of day: 07:30, 12:30, and 16:30 to capture diurnal variations in temperature, humidity, and light intensity. Morning observations represented early post-sunrise conditions, midday measurements coincided with peak solar radiation and heat accumulation, while afternoon readings reflected the declining phase of these parameters.

Due to the limited number of data loggers, sensors were rotated weekly among replicates; however, all measurements were conducted under comparable weather conditions and at consistent times to minimize temporal variation. Although this approach may not fully capture spatial variability, it provides a reasonable representation of relative microclimatic differences among canopy treatments when simultaneous multi-point recording is not feasible. The collected data were then averaged across observation weeks to obtain representative mean values for each treatment.

Morphological characterization of sweet corn

Morphological variables observed included plant height (cm), measured from the soil surface to the tip of the tallest leaf using a measuring tape; leaf number, determined by manual counting of all leaves per plant; and leaf length and width (cm), measured with a ruler from the base to the tip of the leaf and across the widest part of the lamina, respectively. Leaf axilla angle (°) was determined using a

protractor, defined as the angle formed between the main stem and the leaf sheath at the point of leaf emergence.

Morphological and physiological observations of Bird's Eye chili

Morphological variables observed included plant height (cm), measured from the soil surface to the highest growth point using a measuring tape; stem diameter (mm), measured with a digital caliper at 10 cm above the plant base; and leaf area (cm²), quantified using ImageJ software.

Physiological parameters included transpiration rate, photosynthetic rate, internal CO₂ concentration, and stomatal conductance, which were measured using a LI-COR 6800 portable photosynthesis system. All measurements were taken on the third fully expanded leaf from the shoot apex at 10 weeks after planting (WAP), corresponding to the maximum vegetative growth stage of chili plants.

This stage represents the period of peak physiological activity, during which photosynthetic rate, stomatal conductance, and transpiration reach their most stable and representative levels (Raza et al. 2019; Mensah et al. 2023). Single-time-point measurements at the vegetative maximum are commonly used in ecophysiological studies employing the LI-COR system, as they are sufficient to capture treatment and genotypic differences under relatively stable physiological conditions (Fu et al. 2020; Khalid et al. 2019).

Data analysis

Experimental data were analyzed using PKBT-STAT version 3.2 through a one-way Analysis of Variance (ANOVA) under a Randomized Complete Block Design (RCBD), with sweet corn variety as the fixed factor and block as the random factor.

Before ANOVA, data were tested for compliance with statistical assumptions, including normality (Shapiro–Wilk test) and homogeneity of variance (Levene's test). The results confirmed that the data met the assumptions required for ANOVA ($p > 0.05$).

When ANOVA indicated significant or highly significant differences, mean separation was performed using the Honestly Significant Difference (HSD) test at the 5% significance level.

In addition, Pearson's correlation analysis was conducted using RStudio (version 2024.04.0; R Foundation for Statistical Computing, Vienna, Austria) to assess the relationships among physiological and morphological variables.

RESULTS AND DISCUSSION

Effect of sweet corn varieties on the microclimate

The results indicate that differences in sweet corn canopy architecture play a significant role in shaping microclimatic variation beneath the canopy, particularly with respect to light intensity, air temperature, and relative humidity (Figure 2). Varieties with a more open canopy, such as Arinta (J1), generated light conditions close to the

optimal range for chili pepper photosynthesis (35,000–50,000 lux), allowing both chili genotypes, Bonita (shade-loving) and Ori 212 (shade-tolerant), to maintain satisfactory growth despite employing contrasting adaptive strategies. Bonita primarily responded through leaf expansion, whereas Ori 212 preserved physiological stability by maintaining efficient CO₂ utilization (Siahaan et al. 2023).

In contrast, dense-canopied varieties such as Exotic (J2) reduced light intensity to the lower threshold of the optimal range. This condition supported the stable growth of Ori 212, which is more tolerant to shade, while Bonita was still able to adapt by expanding its leaf area, consistent with its characteristic as a shade-loving genotype (Khalid et al. 2019; Wang et al. 2024). The Paragon variety (J4) created a distinct microclimatic condition characterized by lower temperature and higher humidity, combined with more even vertical light distribution resulting from its upright canopy structure. This situation strongly promoted morphological plasticity in Bonita, leading to maximum leaf expansion, while Ori 212 maintained stable growth performance (Raza et al. 2019; Luo et al. 2021).

By contrast, in the open-field control without shading, the combination of elevated temperature, reduced humidity, and excessive light intensity (>60,000 lux) severely suppressed the growth of both chili genotypes, resulting in markedly reduced leaf area and plant height compared with those grown under intercropping conditions. This observation aligns with previous reports that excessive light exposure beyond 60,000 lux induces photoinhibition, reduces photosynthetic efficiency, and increases the risk of oxidative stress (Valverde et al. 2023).

As shown in Table 3, the four sweet corn varieties exhibited significant differences ($p < 0.01$) in plant height, leaf number, leaf blade size, and leaf axil angle. Paragon (J4) recorded the tallest plants (205–209 cm) with relatively narrow leaf angles (24–25°), forming an upright canopy structure that facilitated more uniform vertical light distribution. In contrast, Exotic (J2) showed the shortest plants (168–170 cm) but had the highest number of leaves (11–12), indicating a denser canopy that may reduce light penetration to the understory. Arinta (J1) displayed intermediate height (198 cm) with wider leaf angles (36°), resulting in a more open canopy structure that allowed greater light transmission. Meanwhile, Talenta (J3) exhibited moderate values for both height and leaf angle, representing a balanced canopy architecture.

These morphological differences among varieties correspond well with the observed microclimatic variation in Figure 2, confirming that canopy architecture strongly regulates light interception, air temperature, and relative humidity beneath the canopy. Similar findings were reported by Patandean et al. (2025), who emphasized the importance of canopy diversity in determining light distribution patterns in sweet corn–chili intercropping systems. Likewise, Raza et al. (2019) and Luo et al. (2021) highlighted that variations in canopy structure significantly affect radiation interception and microclimatic regulation in cereal-based intercropping systems.

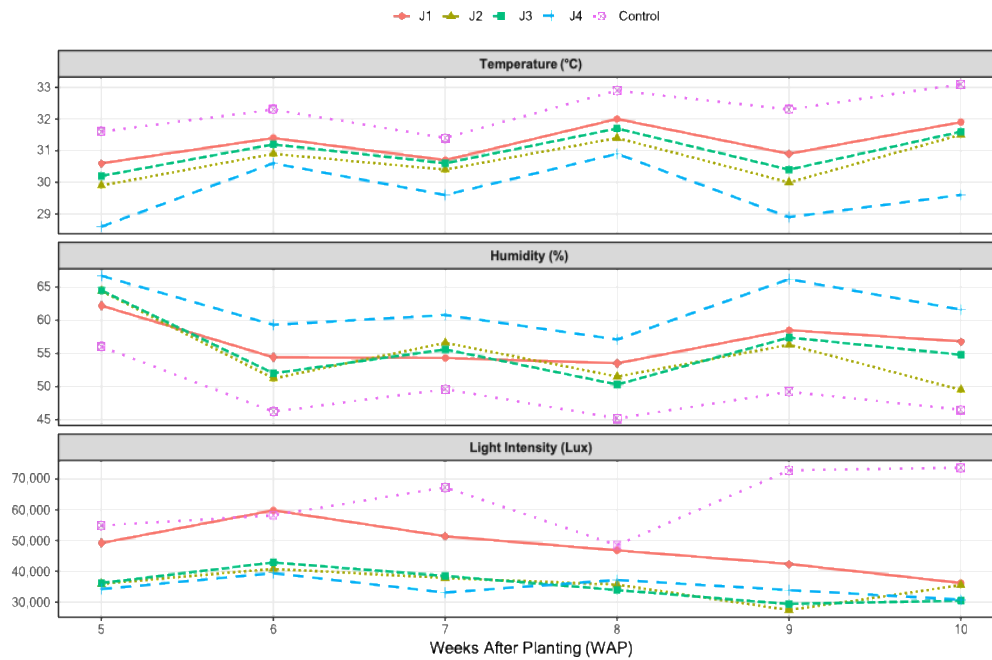


Figure 2. Microclimatic conditions (temperature, relative humidity, and light intensity) under the canopy of four sweet corn varieties. J1: Arinta, J2: Exotic, J3: Talenta, J4: Paragon, compared with open-field control

Table 3. Growth characteristics of four selected sweet corn varieties

Code no.	Characteristic				
	Plant height (cm)	Leaf number (leaves)	Leaf blade length (cm)	Leaf blade width (cm)	Leaf axil angle (°)
J1C1	198.98 ^b	10.67 ^c	89.73 ^c	9.08 ^b	35.87 ^a
J1C2	196.79 ^b	10.83 ^c	91.45 ^c	9.25 ^b	36.46 ^a
J2C1	168.68 ^d	12.75 ^a	99.25 ^{ab}	12.30 ^a	27.56 ^b
J2C2	170.03 ^d	12.42 ^a	101.28 ^a	11.95 ^a	26.94 ^{bc}
J3C1	179.88 ^c	11.67 ^b	93.68 ^{bc}	10.18 ^b	25.93 ^{bcd}
J3C2	182.21 ^c	11.50 ^b	95.23 ^{abc}	9.90 ^b	26.02 ^{bcd}
J4C1	205.62 ^a	10.92 ^c	100.08 ^{ab}	11.55 ^a	24.26 ^d
J4C2	209.78 ^a	10.75 ^c	98.65 ^{ab}	11.73 ^a	24.52 ^{cd}
Sig.	**	**	**	**	**

Note: Values followed by the same letter within the same column are not significantly different according to the Honest Significant Difference (HSD) test at the 5% level. **: Significant at the level of 1%, J1: Sweet corn variety Arinta, J2: Sweet corn variety Exotic, J3: Sweet corn variety Talenta, J4: Sweet corn variety Paragon, C1: Chili pepper variety Bonita, C2: Chili pepper variety Ori 212

Table 4. Plant height, stem diameter, and leaf area of two chili pepper (*Capsicum frutescens*) varieties

Code no.	Characteristic		
	Plant height (cm)	Stem diameter (mm)	Leaf area (cm ²)
J1C1	48.43 ^{ab}	7.58 ^{ab}	13.13 ^{abc}
J1C2	41.10 ^{bc}	7.61 ^{ab}	13.46 ^{abc}
J2C1	59.07 ^{ab}	9.04 ^a	14.04 ^{abc}
J2C2	65.25 ^a	9.17 ^a	19.61 ^{ab}
J3C1	64.66 ^a	8.50 ^a	19.49 ^{ab}
J3C2	56.16 ^{ab}	8.24 ^a	15.39 ^{abc}
J4C1	57.56 ^{ab}	8.08 ^a	20.98 ^a
J4C2	58.73 ^{ab}	8.26 ^a	17.88 ^{ab}
C1	25.33 ^c	5.88 ^{bc}	6.72 ^c
C2	25.99 ^c	5.34 ^c	9.53 ^{bc}
Sig.	**	**	**

Note: Values followed by the same letter within the same column are not significantly different according to the Honest Significant Difference (HSD) test at the 5% level. J1: Sweet corn variety Arinta, J2: Sweet corn variety Exotic, J3: Sweet corn variety Talenta, J4: Sweet corn variety Paragon, C1: Chili pepper variety Bonita, C2: Chili pepper variety Ori 212

Morphological and growth responses of chili pepper (*Capsicum frutescens*) to sweet corn shading (microclimatic conditions)

The results of the Analysis of Variance (ANOVA), followed by the Honest Significant Difference (HSD) test at the 5% significance level, revealed a significant interaction between sweet corn varieties and bird’s eye chili genotypes on chili plant height, stem diameter, and leaf area (Table 4). These results suggest that variation in sweet corn canopy architecture plays an important role in shaping microclimatic conditions, which subsequently influence the adaptive growth strategies of chili plants, consistent with findings in other intercropping systems. In the open-field control, chili growth was suppressed due to excessive light exposure and elevated temperatures, consistent with previous reports indicating that light intensity above the tolerance threshold increases the risk of photoinhibition and reduces photosynthetic efficiency (Gustiar et al. 2023; Siahaan et al. 2023).

Conversely, intercropping with sweet corn, particularly with the Exotic and Talenta varieties, created partial shading conditions that significantly improved chili height, stem diameter, and leaf area. These findings align with agroecological theory, which posits that shading canopies function to stabilize the microclimate by lowering soil temperature, maintaining humidity, and enhancing diffuse light distribution, thereby improving photosynthetic efficiency (Fu et al. 2020; Mensah et al. 2023). Thus, interspecific interactions within intercropping systems are not solely competitive but also involve facilitative mechanisms that support the physiological performance of the understory crop.

The two chili genotypes displayed contrasting adaptive strategies. The shade-loving genotype (C1, Bonita) exhibited greater morphological plasticity, expanding leaf surface area to maximize diffuse light capture. This strategy is consistent with the adaptive responses of horticultural crops that rely on morphological expansion under shaded conditions (Malaviya et al. 2020; Bartkowicz and Paluch 2023). In contrast, the shade-tolerant genotype (C2, Ori 212) demonstrated physiological stability through enhanced radiation use efficiency and regulation of stomatal conductance, enabling consistent growth despite reduced light intensity (Raza et al. 2019). These results highlight a fundamental distinction between shade-loving genotypes,

which adapt via morphological plasticity, and shade-tolerant genotypes, which rely on physiological capacity.

Physiological responses of chili pepper to corn shading

The results demonstrated that among the four physiological parameters observed (photosynthesis, transpiration, stomatal conductance, and CO₂ uptake), only CO₂ uptake differed significantly across treatments ($p < 0.05$), with the highest values recorded under the open control (no shading) and a marked decline under corn canopy conditions (Figure 3). However, CO₂ uptake (represented by internal CO₂ concentration, Ci) should not be interpreted as a direct indicator of photosynthetic performance. Ci reflects the balance between CO₂ diffusion into the leaf and its assimilation in the chloroplasts; hence, a higher Ci value often indicates reduced photosynthetic efficiency or stomatal regulation under stress (Furquhar and Sharkey 1982; Flexas et al. 2004). The reduction in Ci under shaded conditions does not necessarily reflect a decrease in photosynthetic rate, as carbon assimilation is also influenced by internal factors such as mesophyll conductance (Liu et al. 2022) and enzymatic limitations of the Calvin cycle (Márquez et al. 2023). This clarification explains why the higher Ci observed in the control treatment did not correspond to greater net assimilation, since photorespiration tends to be more pronounced under full sunlight (Li et al. 2020).

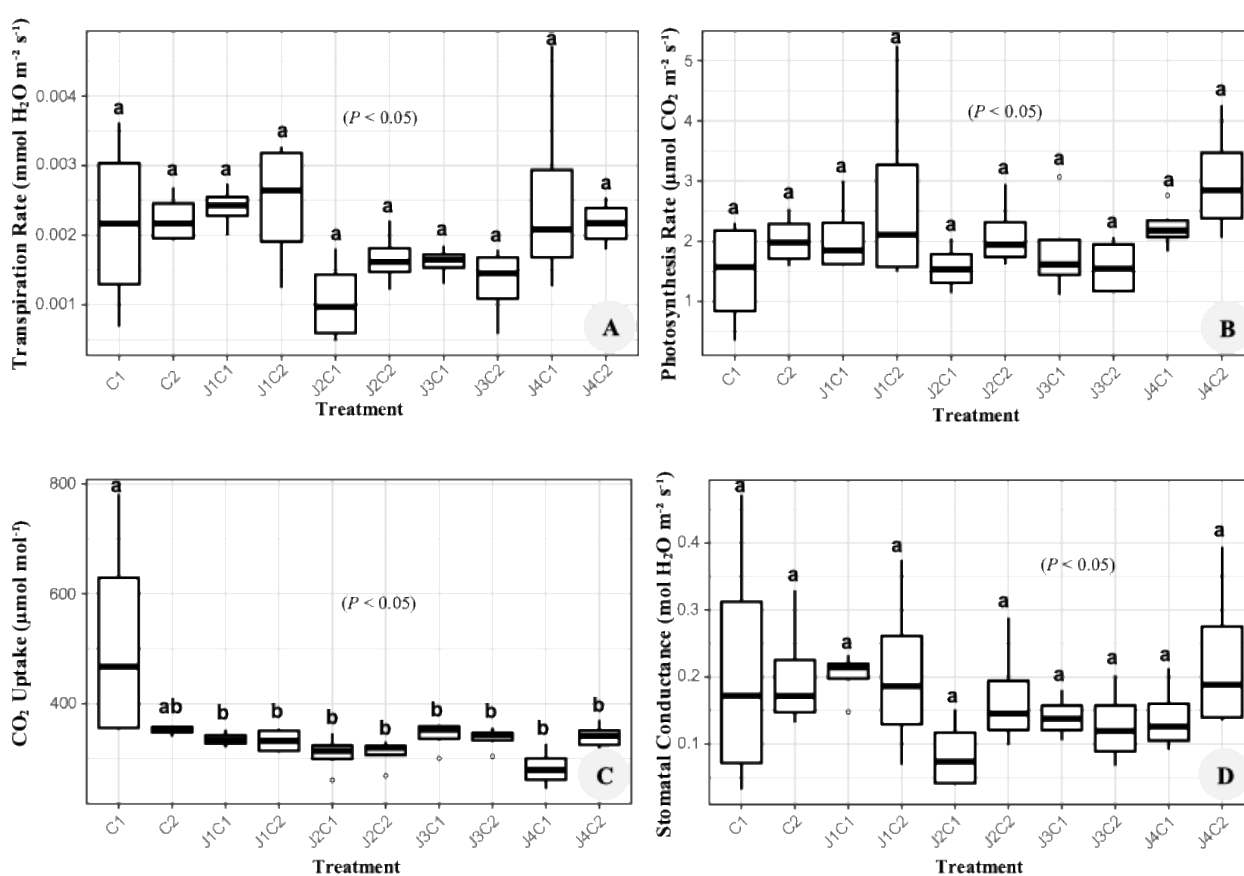


Figure 3. Physiological responses of bird's eye chili genotypes under different sweet corn varieties: A. Transpiration rate (Tr, mmol H₂O m⁻² s⁻¹), B. Net photosynthesis rate (B, μmol CO₂ m⁻² s⁻¹), C. CO₂ uptake (Ci, μmol mol⁻¹) and D. Stomatal conductance (gs, mol H₂O m⁻² s⁻¹). J1: Arinta, J2: Exotic, J3: Talenta, J4: Paragon, C1: Bonita (shade-loving), C2: Ori 212 (shade-tolerant), Control: Open field without corn shading. Different letters indicate significant differences based on ANOVA followed by HSD test at $p < 0.05$

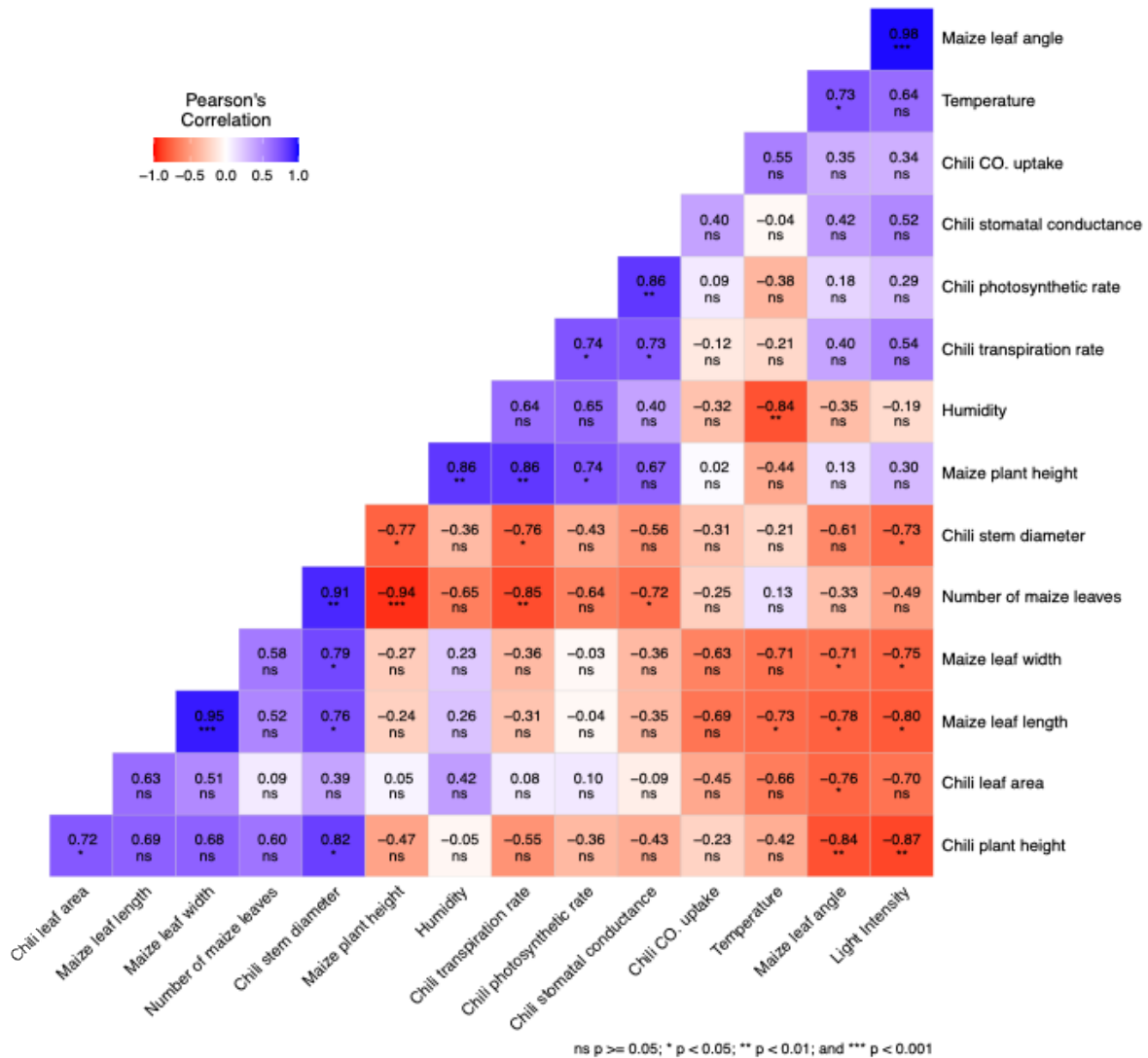


Figure 4. Pearson’s correlation among the quantitative variables of sweet corn and chili pepper

Pearson’s correlation analysis (Figure 4) confirmed significant relationships ($p \leq 0.05$) between microclimatic factors and the physiological responses of chili pepper. Temperature and light intensity exhibited significant negative correlations with photosynthetic rate, stomatal conductance, transpiration, and C_i , whereas relative humidity showed a positive correlation. These results indicate that lower temperature and higher humidity under semi-closed corn canopies improved physiological efficiency by enhancing stomatal conductance and maintaining optimal internal CO_2 balance. Conversely, elevated temperature and excessive light intensity in the unshaded control increased the risk of photoinhibition and suppressed stomatal function. As a result, even though C_i increased, it did not lead to higher net photosynthesis (Valverde et al. 2023; Márquez and Busch 2024).

Differences in adaptive strategies among chili pepper genotypes were also evident in relation to the microclimate. Bonita (shade-loving) displayed a morphological response by expanding leaf area (up to 20.98 cm^2 under Paragon) to maximize diffuse light capture under high humidity and

reduced light intensity. In contrast, Ori 212 (shade-tolerant) maintained physiological efficiency by sustaining relatively stable C_i per unit leaf area, even at lower light intensity (35,000 lux). This stability suggests a greater capacity for CO_2 assimilation efficiency under moderate shading. This pattern aligns with Li et al. (2024), who reported that shade-loving genotypes exhibit stronger morphological plasticity, whereas shade-tolerant genotypes rely primarily on physiological stability.

These findings suggest that variations in sweet corn canopy architecture significantly influence microclimatic regulation and, consequently, the morphophysiological responses of chili pepper. Previous studies on maize-vegetable intercropping (Legba et al. 2025) also highlighted the role of canopy structure in stabilizing temperature and light environments, but they did not differentiate among maize varieties. Our results extend this knowledge by showing that semi-closed canopies (Exotic, Talenta) reduce excessive radiation and favor the growth of the shade-tolerant Ori 212, while the more evenly distributed light environment under Paragon enhances leaf

expansion in Bonita. This genotype-specific compatibility provides new evidence that canopy diversity within a single cereal crop can serve as a driver of resource-use complementarity, thereby advancing precision intercropping strategies in tropical systems.

Implications for intercropping systems and agrobiodiversity

The findings of this study demonstrate that differences in canopy architecture among sweet corn varieties play a direct role in shaping microclimatic variation, which ultimately governs the morphophysiological dynamics of chili pepper. Semi-open canopies, as observed in Exotic (short stature, high leaf number) and Talenta (medium stature with intermediate leaf angle), reduced light intensity to approximately 35,000 lux, an optimal range for shade-tolerant chili genotypes (Siahaan et al. 2023). This condition supported the stable growth of Ori 212, a shade-tolerant variety, consistent with previous reports on *Capsicum annuum* L. intercropping with other companion crops (Wang et al. 2025). Conversely, Paragon, characterized by tall stature and narrow leaf angles, created higher humidity and more uniform vertical light distribution, which strongly benefited Bonita, a shade-loving genotype, through leaf area expansion. These results align with Fu et al. (2020) and Aroca et al. (2023), who emphasized that shade-preferring genotypes rely on morphological flexibility to optimize the absorption of diffuse light.

From an agrobiodiversity perspective, the diversity of sweet corn varieties serves not only as a genetic reservoir but also as an ecological regulator that creates distinct ecophysiological niches for intercrops (Rajametov et al. 2021; Jalloh et al. 2024). Multispecies systems with diverse canopy architectures have been shown to enhance agroecosystem stability (Xiao et al. 2023), improve light-use efficiency (Raza et al. 2019), and mitigate extreme fluctuations in temperature and humidity (Shu et al. 2023). Variation in chili responses to shading morphological plasticity in Bonita and physiological stability in Ori 212 highlights that selecting compatible combinations of shelter crops and intercrops is a key instrument in designing biodiversity-based sustainable farming systems.

The concept of precision intercropping proposed in this study is grounded in aligning corn canopy traits with the adaptive strategies of chili genotypes. The Exotic-Ori 212 and Paragon-Bonita combinations can be positioned as compatible models because they create balanced microclimatic conditions, simultaneously maintaining physiological efficiency and supporting morphological expansion. This approach is consistent with the principles of sustainable intensification, which emphasize interspecific resource complementarity (Van Der Werf et al. 2020; Khanal et al. 2021). Thus, sweet corn varietal diversity contributes not only to enhancing genetic diversity but also functions as a precision ecological strategy to strengthen the resilience of tropical farming systems against environmental stress and climate change (Moore et al. 2022).

Limitations of the study and future research directions

This study was conducted over a single season and at one experimental site with specific agroecological conditions. As such, the results may not fully capture seasonal variability or soil climate interactions present in other environments. Moreover, the controlled research station setting may differ from on-farm conditions, where management intensity and resource availability vary considerably.

To strengthen external validity, future studies should employ multi-season and multi-location trials, particularly across diverse agroecological zones in the tropics. On-farm validation is essential to test the feasibility of genotype canopy matching under farmer-managed systems. In addition, integrating physiological measurements with canopy modeling or crop simulation tools could help predict intercropping outcomes across environments. Such approaches will enhance the translation of experimental findings into scalable recommendations for sustainable intensification and biodiversity conservation.

In conclusion, this study demonstrates that variations in sweet corn canopy architecture significantly influence the microclimate, which consequently affects the morphophysiological responses of intercropped chili pepper. Varieties with semi-open canopies, such as Exotic and Talenta, created favorable microclimatic conditions that enhanced the performance of the shade-tolerant chili genotype (Ori 212), while Paragon supported the shade-loving genotype (Bonita) by maintaining higher humidity and more uniform light distribution. In contrast, the dense canopy of Arinta limited light penetration, resulting in reduced chili growth. These findings suggest that canopy diversity among corn varieties can be utilized to optimize microclimate conditions and improve intercrop compatibility. Nevertheless, since this experiment was conducted at a single site and during one growing season, further research across multiple environments and seasons is required to validate these results and to better understand their implications for long-term productivity and agrobiodiversity enhancement.

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REFERENCES

- Aroca A, García-Díaz I, García-Calderón M, Gotor C, Márquez AJ, Betti M. 2023. Photorespiration: Regulation and new insights on the potential role of persulfidation. *J Exp Bot* 74 (19): 6023-6039. DOI: 10.1093/jxb/erad291.
- Arta IMSD, Chozin MA, Ritonga AW. 2024. Evaluation of growth and yield potential of three varieties of chili pepper (*Capsicum frutescens*)

- intercropped with maize (*Zea mays*) at different planting times. *Biodiversitas* 25 (10): 3985-3994. DOI: 10.13057/biodiv/d251058.
- Bartkowiec L, Paluch J. 2023. Morphological plasticity of six tree species with different light demands growing in multi-layered deciduous forests in Central Europe. *Eur J For Res* 142: 1177-1195. DOI: 10.1007/s10342-023-01584-7.
- Bechem EE, Ojong AN, Etchu KA. 2018. The effects of intercropping and plant densities on growth and yield of maize (*Zea mays* L.) and soybean (*Glycine max*) in the humid forest zone of Mount Cameroon. *Afr J Agric Res* 13 (12): 574-587. DOI: 10.5897/ajar2017.12895.
- Chen G, Liu M, Zhao X, Bawa G, Liang B, Feng L, Pu T, Yong T, Liu W, Liu J, Du J, Yang F, Wu Y, Liu C, Wang X, Yang W. 2024. Improved photosynthetic performance under unilateral weak light conditions in a wide-narrow-row intercropping system is associated with altered sugar transport. *J Exp Bot* 75 (1): 258-273. DOI: 10.1093/jxb/erad370.
- Deng F, Li B, Yuan Y, He C, Zhou X, Li Q, Zhu Y, Huang X, He Y, Ai X, Tao Y, Zhou W, Wang L, Cheng H, Chen Y, Wang M, Ren W. 2022. Increasing the number of seedlings per hill with a reduced number of hills improves rice grain quality by optimizing canopy structure and light utilization under shading stress. *Field Crops Res* 287: 108668. DOI: 10.1016/j.fcr.2022.108668.
- Flexas J, Bota J, Loreto F, Cornic G, Sharkey TD. 2004. Diffusive and metabolic limitations to photosynthesis under drought and salinity in C_3 plants. *Plant Biol* 6: 269-279. DOI: 10.1055/s-2004-820867.
- Fu J, Luo Y, Sun P, Gao J, Zhao D, Yang P, Hu T. 2020. Effects of shade stress on turfgrasses' morphophysiology and rhizosphere soil bacterial communities. *BMC Plant Biol* 20 (1): 92. DOI: 10.1186/s12870-020-2300-2.
- Furquhar GD, Sharkey TD. 1982. Stomatal conductance and photosynthesis. *Ann Rev Plant Physiol* 33: 317-345. DOI: 10.1146/annurev.pp.33.060182.001533.
- Gustiari F, Lakitan B, Budianta D, Negara ZP. 2023. Assessing the impact on growth and yield in different varieties of chili pepper (*Capsicum frutescens*) intercropped with chaya (*Cnidoscolus aconitifolius*). *Biodiversitas* 24 (5): 2639-2646. DOI: 10.13057/biodiv/d240516.
- Jalloh AA, Mutyambai DM, Yusuf AA, Subramanian S, Khamis F. 2024. Maize edible-legumes intercropping systems for enhancing agrobiodiversity and belowground ecosystem services. *Sci Rep* 14 (1): 14355. DOI: 10.1038/s41598-024-64138-w.
- Khalid MHB, Raza MA, Yu HQ, Sun FA, Zhang YY, Lu FZ, Si L, Iqbal N, Khan I, Fu FL, Li WC. 2019. Effect of shade treatments on morphology, photosynthetic, and chlorophyll fluorescence characteristics of soybeans (*Glycine max* L. Merr.). *Appl Ecol Environ Res* 17 (2): 2551-2569. DOI: 10.15666/aecer/1702_25512569.
- Khanal U, Stott KJ, Armstrong R, Nuttall JG, Henry F, Christy BP, Mitchell M, Riffkin PA, Wallace AJ, McCaskill M, Thayalakumaran T, O'Leary GJ. 2021. Intercropping: Evaluating the advantages to broadacre systems. *Agriculture* 11 (5): 453. DOI: 10.3390/agriculture11050453.
- Lan Y, Zhang H, He Y, Jiang C, Yang M, Ye S. 2023. Legume-bacteria-soil interaction networks linked to improved plant productivity and soil fertility in intercropping systems. *Ind Crops Prod* 196: 116504. DOI: 10.1016/j.indcrop.2023.116504.
- Legba EC, Dossou L, Honfoga J, Pawera L, Srinivasan R. 2025. Productivity and profitability of maize-mungbean and maize-chili pepper relay intercropping systems for income diversification and soil fertility in southern Benin. *Sustainability* 17. DOI: 10.3390/su17031076.
- Li C, Stomph T-J, Makowski D, Li H, Zhang C, Zhang F, van der Werf W. 2023. The productive performance of intercropping. *Proc Natl Acad Sci USA* 120 (2): e2201886120. DOI: 10.1073/pnas.2201886120.
- Li Y, Xin G, Liu C, Shi Q, Yang F, Wei M. 2020. Effects of red and blue light on leaf anatomy, CO₂ assimilation, and the photosynthetic electron transport capacity of sweet pepper (*Capsicum annuum* L.) seedlings. *BMC Plant Biol* 20 (1): 318. DOI: 10.1186/s12870-020-02523-z.
- Li Y, Zhao J, Ma H, Pu L, Zhang J, Huang X, Yang H, Fan G. 2024. Shade tolerance in wheat is related to photosynthetic limitation and morphological and physiological acclimation. *Front Plant Sci* 15: 1465925. DOI: 10.3389/fpls.2024.1465925.
- Liu T, Barbour MM, Yu D, Rao S, Song X. 2022. Mesophyll conductance exerts a significant limitation on photosynthesis during light induction. *New Phytol* 233 (1): 360-372. DOI: 10.1111/nph.17757.
- Luo C, Guo Z, Xiao J, Dong K, Dong Y. 2021. Effects of the applied ratio of nitrogen on the light environment in the canopy and growth, development, and yield of wheat when intercropped. *Front Plant Sci* 12: 719850. DOI: 10.3389/fpls.2021.719850.
- Malaviya DR, Baig MJ, Kumar B, Kaushal P. 2020. Effects of shade on guinea grass genotypes *Megathyrsus maximus* (Poales: Poaceae). *Rev Biol Trop* 68 (2): 563-572. DOI: 10.15517/rbt.v68i2.38362.
- Márquez DA, Busch FA. 2024. The interplay of short-term mesophyll and stomatal conductance responses under variable environmental conditions. *Plant Cell Environ* 47 (9): 3393-3410. DOI: 10.1111/pce.14880.
- Márquez DA, Stuart-Williams H, Cernusak LA, Farquhar GD. 2023. Assessing the CO₂ concentration at the surface of photosynthetic mesophyll cells. *New Phytol* 238 (4): 1446-1460. DOI: 10.1111/nph.18784.
- Mensah EO, Ræbild A, Asare R, Amoatey CA, Markussen B, Owusu K, Asitoakor BK, Vaast P. 2023. Combined effects of shade and drought on physiology, growth, and yield of mature cocoa trees. *Sci Total Environ* 899: 165657. DOI: 10.1016/j.scitotenv.2023.165657.
- Moore VM, Schlautman B, Fei S-Z, Roberts LM, Wolfe M, Ryan MR, Wells S, Lorenz AJ. 2022. Plant breeding for intercropping in temperate field crop systems: A review. *Front Plant Sci* 13: 843065. DOI: 10.3389/fpls.2022.843065.
- Patandean B, Chozin MA, Ritonga AW. 2025. Diversity of sweet corn canopy architecture for intercropping pattern suitability with cayenne pepper. *J Trop Crop Sci* 12 (2): 314-326. DOI: 10.29244/jtcs.12.02.314-326.
- Peng Z, Zhang Y, Yan B, Zhan Z, Chi X, Xu Y, Guo X, Cui X, Wang T, Wang S, Kang C, Wan X, Sun K, Huang L, Guo L. 2021. Diverse intercropping patterns enhance the productivity and volatile oil yield of *Atractylodes lancea* (Thunb.) DC. *Front Plant Sci* 12: 663730. DOI: 10.3389/fpls.2021.663730.
- Rajameto V, Yang EY, Cho MC, Chae SY, Jeong HB, Chae WB. 2021. Heat-tolerant hot pepper exhibits constant photosynthesis via increased transpiration rate, high proline content, and fast recovery in heat stress conditions. *Sci Rep* 11 (1): 14328. DOI: 10.1038/s41598-021-93697-5.
- Raza MA, Feng LY, Iqbal N, Ahmed M, Chen YK, Khalid MHB, Din AMU, Khan A, Ijaz W, Hussain A, Jamil MA, Naem M, Bhutto SH, Ansar M, Yang F, Yang W. 2019. Growth and development of soybean under changing light environments in a relay intercropping system. *PeerJ* 7: e7262. DOI: 10.7717/peerj.7262.
- Revilla P, Anibas CM, Tracy WF. 2021. Sweet corn research around the world 2015-2020. *Agronomy* 11 (3): 534. DOI: 10.3390/agronomy11030534.
- Ruswandi D, Yuwariah Y, Arianti M, Syafii M, Nuraini A. 2020. Stability and adaptability of yield among early sweet corn hybrids in West Java, Indonesia. *Intl J Agron* 2020 (1): 4341906. DOI: 10.1155/2020/4341906.
- Shu G, Wang A, Wang X, Chen R, Gao F, Wang A, Li T, Wang Y. 2023. Identification of QTNs, QTN-by-environment interactions for plant height and ear height in maize multi-environment GWAS. *Front Plant Sci* 14: 1284403. DOI: 10.3389/fpls.2023.1284403.
- Siahaan GF, Chozin MA, Syukur M, Ritonga AW. 2023. Estimation of genetic parameters and variability of various cayenne peppers under net shading. *Biodiversitas* 24 (11): 5912-5919. DOI: 10.13057/biodiv/d241109.
- Valverde BM, Gómez-Merino FC, Corona-Torres T, Mateos-Nava RA, Trejo-Téllez LI. 2023. Effects of cadmium, thallium, and vanadium on photosynthetic parameters of three chili pepper (*Capsicum annuum* L.) Varieties. *Plants* 12 (20): 3563. DOI: 10.3390/plants12203563.
- Van Der Werf W, Li C, Cong W-F, Zhang F. 2020. Intercropping enables a sustainable intensification of agriculture. *Front Agric Sci Eng* 7 (3): 254-256. DOI: 10.15302/j-fase-2020352.
- Wang C, Heng Y, Xu Q, Zhou Y, Sun X, Wang Y, Yao W, Lian M, Li Q, Zhang L, Niinemets Ü, Hölscher D, Gielis J, Niklas KJ, Shi P. 2024. Scaling relationships between the total number of leaves and the total leaf area per culm of two dwarf bamboo species. *Ecol Evol* 14 (7): e70002. DOI: 10.1002/ece3.70002.
- Wang J, Wang Q, Gao J et al. 2025. Genetic regulatory pathways of plant flowering time affected by abiotic stress. *Plant Stress* 15 (1): 100747. DOI: 10.1016/j.stress.2025.100747.
- Wang L, Geilfus C-M, Sun T, Zhao Z, Li W, Zhang X, Wu X, Tan D, Liu Z. 2023. Double gains: Boosting crop productivity and reducing carbon footprints through maize-legume intercropping in the Yellow

- River Delta, China. *Chemosphere* 344: 140328. DOI: 10.1016/j.chemosphere.2023.140328.
- Widyaningsih N, Susila WA, Khumaira A. 2021. *Bacillus* sp. effectivity test as a growth suppressor agent from antrachnose disease caused by *Colletotrichum* sp. on cayenne pepper plant (*Capsicum frutescens* L.). *Intl J Health Sci Technol* 3 (1): 150-158. DOI: 10.31101/ijhst.v3i1.2241.
- Xiang Q, Guo W, Tang X, Cui S, Zhang F, Liu X, Zhao J, Zhang H, Mao B, Chen W. 2021. Capsaicin, the spicy ingredient of chili peppers: A review of the gastrointestinal effects and mechanisms. *Trends Food Sci Technol* 116: 755-765. DOI: 10.1016/j.tifs.2021.08.034.
- Xiao X, Han L, Chen H, Wang J, Zhang Y, Hu A. 2023. Intercropping enhances microbial community diversity and ecosystem functioning in maize fields. *Front Microbiol* 13: 1084452. DOI: 10.3389/fmicb.2022.1084452.
- Zubay P, Ruttner K, Ladányi M, Deli J, Zámboriné ÉN, Szabó K. 2021. In the shade - Screening of medicinal and aromatic plants for temperate zone agroforestry cultivation. *Ind Crops Prod* 170: 113764. DOI: 10.1016/j.indcrop.2021.113764.