

Phenological, growth, and yield responses of sweet corn to elevational air temperatures in the humid tropics

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Abstract

Temperature plays a determinant role in the rate of plant metabolic activities and, accordingly, dictates the plant's phenological stages, growth, and productivity. The objective of this study was to evaluate the phenological, growth, and ear yield behavior of ten sweet corn hybrids in response to elevational temperature changes in the humid tropics. Seeds of ten hybrids were grown in three elevations (coastland, midland, and highland). Results show that the hybrids belonged to the same maturity group with comparable accumulated growing degree days, but they varied in green ear yield, harvest index, and heat use efficiency. It was also found that higher elevations lead to longer plant growth and fewer growing degree-day requirements, resulting in increased biomass accumulation for ear and overall vegetative growth but more efficient in the heat use. These findings will be useful as a guide for crop management scheduling, including fertilizers application, pest control, diseases control, and weed control, to maximize sweet corn yield at different elevations in the humid tropics.

Keywords: biological yield, harvest index, heat use efficiency, marketable ear yield, photosynthate.

Abbreviations: GDD_growing degree days; HUE_heat use efficiency; GEY_green ear yield; BioY_biological yield; HI_harvest index.

Introduction

Sweet corn (*Zea mays* L. *saccharata* Sturt.) is a specialty maize species grown particularly for human consumption, as either a fresh or a processed product. The kernels of sweet corn in the early dough stage can serve as a source of minerals, vitamins, antioxidants, and fiber (Swapna et al., 2020). Planted area of sweet corn is spread over from 58°N to 40°S latitude, at sea level to 3000 m above sea level, and in dry to humid climates (Tracy, 1993). However, its growth and development are significantly influenced by the characteristics of climate components inherent in the growing areas, especially temperature, solar radiation, sunshine duration, photoperiod, and precipitation (Liu et al., 2013; Tsimba et al., 2013). Of these components, temperature is the most influential on the sweet corn's developmental rate (Olsen et al., 1993; Khan et al., 2011; Rosa et al., 2016).

Temperature plays a primary factor in the rate and timing of plant physiological processes, and thus the growth and development of the plant. Each phenological stage has its own heat requirements, and to reach a certain phenological stage, the plant has to accumulate the required heat units (Miller et al., 2001). Inappropriate temperature at specific growth stages will so inhibit plant growth and development and even reduce yield (Williams, 2008). As a warm-climate crop with C4 photosynthetic pathway, sweet corn requires high temperatures for optimal germination and further development. Kara (2011) noted that as the air temperature increased between 10°C and 30°C, the rate of plant development increased almost linearly. However,

temperatures above 35°C are generally detrimental to photosynthesis and reproductive development (Tracy et al., 2020).

Temperature is frequently studied in terms of the heat utilization index, including the growing degree days (GDD) and heat use efficiency (HUE). These indices have frequently been used to assess changes in the phenology and growth behavior of plants at a given agro-ecosystem ambient temperature and thus provide reliable predictions of crop development with respect to crop management scheduling (Sree et al., 2018; Weber et al., 2015). GDD refers to the total effective heat accumulation between plant phenological stages, which in turn can be used to predict when a particular plant stage will occur given a known daily temperature (Burhan, 2011; Vafa et al., 2014). In sweet corn production, its application mainly lies in estimating how long it takes for the crop to reach a phenological stage of interest such as emergence, vegetative, generative, and harvesting (Williams, 2014; Jan et al., 2022). Other applications include determining the best times for sowing seeds, irrigation, fertilization, weeding, and insect management (Tursun et al., 2016; Banotra et al., 2017; Ahmad et al., 2022). HUE, on the other hand, measures the capacity of the plant to obtain biomass or marketable yield per unit of GDD. (Kumar and Kumar, 2014; Devi et al., 2019; Jan et al. 2022). A higher HUE indicates that plant made use of the heat more efficiently by increasing biological activity and higher biomass accumulation. Therefore, heat use efficiency (HUE) is useful

for assessing the yield potential of a crop in a given environment (Singh et al., 2018).

In tropical regions, such as Indonesia, the mean monthly temperatures are consistently high, averaging 25 to 28 °C, with cooler temperatures occurring at higher elevations. Such a range of temperatures favors sweet corn growth year-round. Even so, the rate of development and yield can vary among genotypes in response to differences in air temperature (Khan et al., 2009). Few, if any, studies have specifically addressed the behavior of sweet corn in response to temperature changes along tropical elevation gradients. This kind of study will bring a new perspective to improving crop management in the regions. The present study was performed to evaluate the phenological, growth, and ear yield behavior of sweet corn hybrids in response to elevational temperature changes in the humid tropics of Indonesia.

Results and Discussion

Phenological pattern

Based on the analysis of variance in the timing of plant phenological development, effects of hybrid and elevation interactions ($p < 0.05$) were found only on VE, V5, V10, and R4, implying that the relative rank of hybrids varied with elevation at these phenological stages. However, since at each corresponding elevation, the slowest and fastest hybrids in reaching each of these stages were only distinguished by no more than 4 days, the change in hybrids' ranking across elevations would be equivocal and less pronounced in a practical sense. Moreover, the variability between the hybrids was also low in all remaining phenological stages ($p > 0.05$). Table 1 lists the average duration to reach the phenological stages displayed by the hybrids from the three elevations, suggesting that all hybrids belong to a common maturity group (Olsen et al., 1993; Wiley et al., 2021).

In addition to these facts, elevation changes affected all phenological stages ($p < 0.01$). Figure 1 depicts the phenological response of the tested hybrids to the elevation difference. In all cases, the coastal environment stimulated the plants to attain maturity earlier than in midland and highland environments. Likewise, plants in the midland environment mature earlier than those in the highland environment, although they are just as fast in the late vegetative and early reproductive stages. These findings imply that, until the optimal temperature is reached, the rate of development increases with increasing temperature. Using the dough stage as a reference, the harvest of fresh ears can be conducted in highland, midland, and coastal environments as the plants reach 85.0, 78.8, and 70.6 DAS, respectively. In other words, with each declining elevation, the harvest date can be moved forward, and in this case, by about a week.

Heat accumulation / growing degree days

There was no interactive effect of hybrid and elevation on growing degree days (GDD) in each phenological stage ($p > 0.05$). Similarly, no variation was observed between the hybrids ($p > 0.05$). Table 2 lists the average GDD accumulated at each phenological stage by hybrids from three elevations. This signifies that all hybrids had comparable heat utilization during the growing season, which varied between 1156.4 °C d and 1173.8 °C d, implying no difference in timing for cultural management regardless

of the choice of the hybrid. These GDD values are also in the range of those reported by Burhan (2011) and Hussain et al. (2022).

In terms of phenological development timing, elevation changes influenced GDD at all observed phenological stages ($p < 0.05$). However, the difference in GDD between elevations did not remain constant throughout the stages. Figure 2 shows the difference in heat accumulated by plants at the three elevations was not as large during the vegetative phase, but became greater during the later phase, as also reported by Hamid et al. (2020). The maximum GDD sowing to harvest was 1260.4 °C d in the coastland environment, followed by 1208.6 °C d in the midland, and 1024.9 °C d in the highland. These discrepancies corroborate the findings of Grigorieva (2020) and Jung et al. (2016) that GDD values are linked to the spatial and temporal distribution of the climatic variables in the geographic areas of crop growing.

Photosynthate partitioning and heat use efficiency

Green ear yield (GEY), biological yield (BioY), harvest index (HI), and heat use efficiency (HUE) were affected by the hybrids and the elevations ($p < 0.05$), but not the interaction of both factors. Although all hybrids had similar phenological timings and heat requirements, they appeared to have different capacities in photosynthate production and partitioning, as well as harvesting biomass per unit of heat use (Table 3). GEY, as the manifestation of photosynthate allocated for reproductive organs, was averaged between 18.4 t/ha and 24.8 t/ha. On the other hand, the whole plant photosynthetic accumulation, manifested as BioY, was averaged between 44.5 t/ha and 54.1 t/ha. These are comparable to those reported by Shetye et al. (2018). HI of sweet corn is frequently observed to be greater than 35% and, in some cases, below this value (Peykarestan et al., 2018; Rajablarjani et al., 2014; Swamy et al., 2016). In the present study, the HI of the hybrids varied between 39.7% and 47.8%, which would be of considerable advantage to help determine the most effective hybrids in partitioning their accumulated resources into harvestable yields. Similarly, the HUE of the hybrids was observed between 16.0 (kg/ha)/ °C d and 21.7 (kg/ha)/ °C d. The greater the value of HUE, the more vigorous and productive the plant (Jan et al., 2022). Taking all these characteristics into consideration, hybrid 5 (Caps 5 x Caps 22) should be regarded as a superior genotype for having higher GEY, BioY, HI, and HUE, followed by hybrid 4 (Caps 5 x Caps 17B) and hybrid 7 (Caps 17A x Caps 17B).

The lower temperature found in the highlands did prolong plant development and reduce GDD considerably, but plants appeared to gain benefits from this phenomenon. The plants grown in the highlands produced the highest GEY and BioY, followed by the midland (Figure 3A and figure 3B). With prolonged development and consequently longer growth, plants are able to maintain their photosynthetic activity for a longer period of time and create more photosynthate. In addition, lower temperatures with increasing altitude would limit the recent consumption of photosynthate (sugars) for respiration, allowing for a greater allocation to biomass formation, as hypothesized by Collalti et al. (2020). In other words, a lower respiration rate (sugar consumption) compared to photosynthesis (sugar production) is generally considered beneficial for maximizing crop productivity (Lutt et al., 2016). This is supported by the higher HUE value

Table 1. The number of days required from sowing to reach certain phenological stages at three elevations in the humid tropics, including emergence (VE), third leaf (V3), fifth leaf (V5), tenth leaf (V10), tasseling (VT), silking (R1), blistering (R2), milk (R3), and dough (R4) stages.

Hybrid	VE	V3	V5	V10	VT	R1	R2	R3	R4
— days after sowing —									
1	5.1	10.3	14.3	35.4	50.7	51.8	62.2	72.9	78.3
2	5.3	11.1	15.6	36.6	51.7	52.4	63.3	73.1	78.6
3	5.0	10.6	14.9	35.4	51.1	52.3	63.2	72.7	77.8
4	5.1	10.7	16.1	37.4	52.0	53.1	63.3	73.1	78.7
5	5.1	10.7	14.7	35.9	50.8	52.0	63.1	73.4	78.4
6	4.9	10.3	14.3	35.2	50.6	51.6	62.9	72.8	77.7
7	5.0	10.9	14.9	36.1	50.9	52.2	63.2	72.8	77.8
8	5.0	10.4	14.8	35.8	50.8	52.0	62.7	72.8	77.8
9	5.1	10.7	14.8	35.4	50.3	51.9	62.6	72.4	77.9
10	4.7	10.3	14.7	35.7	51.0	52.1	63.4	72.9	78.3

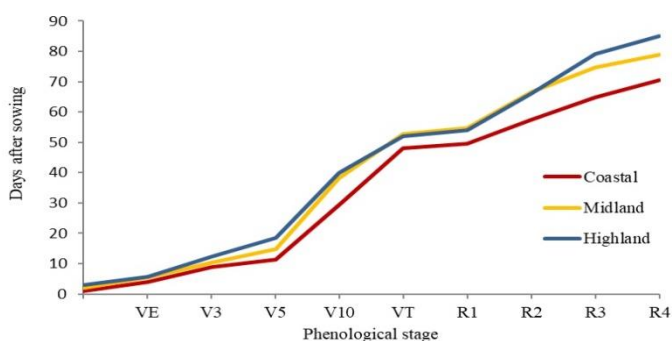


Figure 1. The number of days required from sowing to reach certain phenological stages at three elevations in the humid tropics, including emergence (VE), third leaf (V3), fifth leaf (V5), tenth leaf (V10), tasseling (VT), silking (R1), blistering (R2), milk (R3), and dough (R4) stages.

Table 2. GDD accumulated by sweet corn hybrids over three elevations in the humid tropics to achieve different stages of phenology, including emergence (VE), third leaf (V3), fifth leaf (V5), tenth leaf (V10), tasseling (VT), silking (R1), blistering (R2), milk (R3), and dough (R4) stages.

Hybrid	VE	V3	V5	V10	VT	R1	R2	R3	R4
— °C days —									
1	91.4	167.5	223.9	539.3	769.2	787.3	936.5	1086.3	1171.2
2	95.0	180.1	242.0	555.9	785.1	797.2	952.6	1090.1	1170.4
3	90.0	171.0	232.0	545.5	776.5	797.7	952.7	1083.8	1159.1
4	91.1	172.7	229.8	550.1	787.5	813.4	952.7	1092.0	1173.8
5	91.4	172.4	228.4	545.9	771.0	787.0	950.4	1096.5	1169.6
6	88.5	167.5	223.9	536.1	767.2	782.8	945.1	1085.0	1156.4
7	90.4	176.6	232.4	549.3	771.8	793.6	951.6	1084.1	1158.7
8	89.7	169.3	230.4	544.3	770.8	789.3	943.1	1084.8	1158.8
9	91.4	172.2	229.8	542.6	764.1	785.4	942.6	1080.3	1161.0
10	85.5	167.9	228.8	542.6	767.2	792.3	955.5	1086.3	1167.5

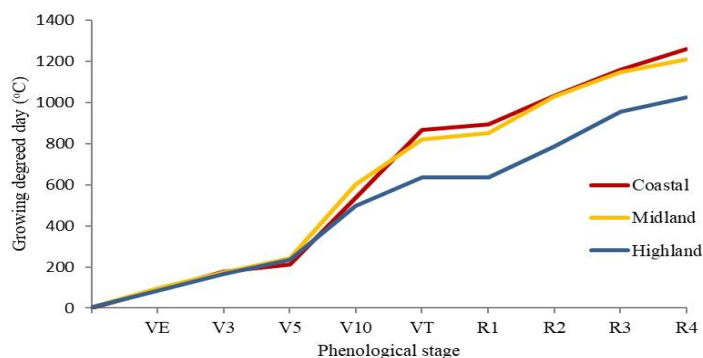


Figure 2. GDD accumulated by sweet corn hybrids for attaining different stages of phenology at three elevations in the humid tropics, including emergence (VE), third leaf (V3), fifth leaf (V5), tenth leaf (V10), tasseling (VT), silking (R1), blistering (R2), milk (R3), and dough (R4) stages.

Table 3. Mean green ear yield (GEY), biological yield (BioY), harvest index (HI), and heat use efficiency (HUE) of sweet corn hybrids over three elevations in the humid tropics. Mean values followed by the same letter within a column are not significantly different at $p < 0.05$ based on LSD multiple comparisons.

Hybrid	GEY (t/ha)	BioY (t/ha)	HI (%)	HUE (kg/ha)/°C d
1	22.6 bc	54.1 a	42.3 bc	19.6 bcd
2	18.4 f	44.5 d	41.8 c	16.0 g
3	21.8 cd	52.9 abc	41.6 c	19.0 cde
4	23.0 bc	48.8 cd	47.5 a	20.1 b
5	24.8 a	53.7 ab	47.1 a	21.7 a
6	21.3 de	45.0 d	47.8 a	18.7 def
7	23.0 bc	51.4 abc	45.5 ab	20.2 b
8	22.7 bc	49.6 bc	46.0 a	19.9 bc
9	20.4 e	51.5 abc	39.7 c	17.9 f
10	21.0 de	50.9 abc	41.8 c	18.2 ef

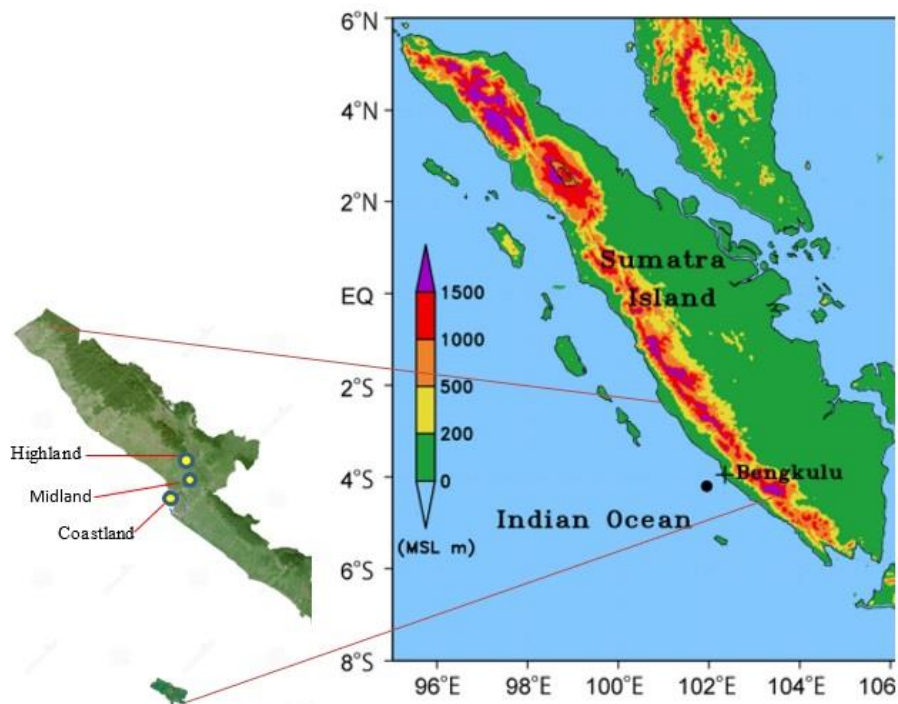


Figure 3. Map of study area.

Table 4. The weather data for experimental fields during the growing season.

No	Location	Climatic component	Month			
			August	September	October	November
1	Coastland 3°52.39'S; 102°19.17'E	Mean daily temperature (°C)	26.7	26.9	26.7	27.0
		Mean daily relative humidity (%)	84.6	84.2	85.1	82.3
		Monthly precipitation (mm)	213	262	421	258
2	Midland 3°29.33'S; 102°30.77'E	Mean daily temperature (°C)	25.4	25.3	25.3	24.9
		Mean daily relative humidity (%)	73.4	76.3	79.5	78.5
		Monthly precipitation (mm)	159.0	343.5	332.6	267.0
3	Highland 3°27.32'S; 102°36.78'E	Mean daily temperature (°C)	21.9	22	21.6	21.9
		Mean daily relative humidity (%)	81.2	83.8	84.5	82
		Monthly precipitation (mm)	256.5	323.8	347.7	299.6

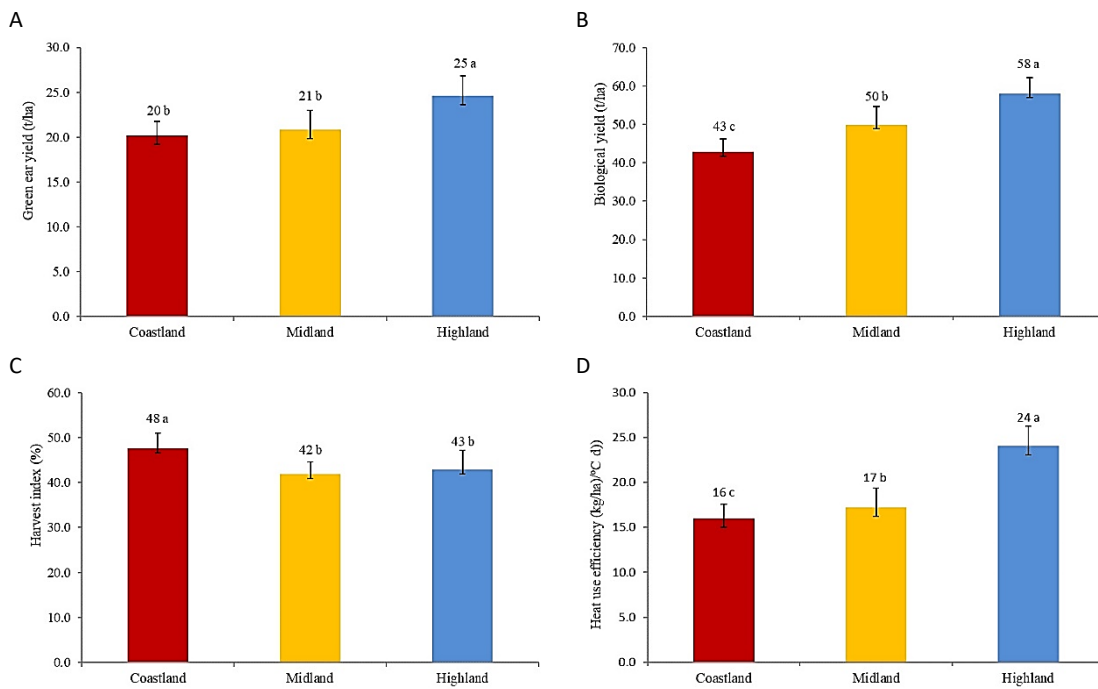


Figure 4. The geographical location of the experimental sites.

found in the highlands, which decreased gradually as elevation decreased (Figure 3C). In terms of HI, plants grown in the highlands and midlands appeared to allocate a lesser amount of their accumulated photosynthate to ear development than plants planted on the coastland (Figure 3D). These findings suggest that temperature has a direct effect on the partitioning of accumulated photosynthate to ear expansion or kernel growth. All of the hybrids under evaluation were developed in highland climates and are expected to be well adapted to low temperatures. As the temperature increased along with decreased elevations, the development rate accelerated, resulting in shorter vegetative and reproductive phases (Figure 1). Consequently, the rate of photosynthate translocation for grain filling increased, but the grain filling period shortened (Muchow, 1990; Wang et al., 2023). The present findings are very similar to those reported by Lafitte and Edmeades (1997), who found that the HI of highland corn varieties declined as site temperature increased, while the opposite was true for lowland varieties. The results of this study have several important implications for better crop management decisions to maximize yields of sweet corn in the humid tropics. They can be used as the reference for scheduling fertilizers application (Jafarikouhini et al., 2020), pest control (Gagnon et al., 2019; Rhino et al., 2019), diseases control (Terefe et al., 2023) and weed control (Tursun et al., 2016; Hussen, 2021). To gain more in-depth understanding, the direct effects of temperature on dry matter production and partitioning to the ear and other organs must be considered in future efforts to relate sweet corn performances to the elevational temperature of the tropics.

Materials and Methods

Experimental sites

Bengkulu Province is located on the southwest coast of Sumatra Island, Indonesia. It has three main physiographic regions: coastland along the West Coast; midland in the Central Region; and highland in the Bukit Barisan Mountain

Range. The study was conducted from August to November 2021 in three locations with different elevations in Bengkulu Province, namely the coastland of Bengkulu City (10 m), the midland of Kepahiang Regency (600 m), and the highland of Rejang Lebong Regency (1050 m). Figure 4, as adapted from Wu et al. (2018) shows the geographical position of the experimental sites. The weather data during the growing season for each location are presented in Suppl Table 1 and summarized in Table 4, indicating that temperature was the main discriminating weather component among the locations. The initial soil analysis indicated that the three experimental sites had comparable chemical and physical characteristics, although they relatively differed in texture (Suppl Table 2).

Planting materials

The planting materials used in present study were seeds of ten experimental hybrids selected from a half-diallel cross of advanced sweet corn inbred lines (Suppl Table 3). These were (1) Caps 2 x Caps 17A, (2) Caps 3 x Caps 17A, (3) Caps 3 x Caps 17B, (4) Caps 5 x Caps 17B, (5) Caps 5 x Caps 22, (6) Caps 15 X Caps 22, (7) Caps 17A x Caps 17B, (8) Caps 17A x Caps 22, (9) Caps 17B x Caps 23, and (10) Caps 22 x Caps 23. The crosses were made in the preceding season of the present trial. Both inbred lines and their hybrids were developed in the breeding station located in the highland of Rejang Lebong Regency.

Experimental setup

A completely randomized block design with three replications was set up to allocate the hybrids to the experimental plots at each location. The experimental plot was a 5-m-long twin-row spaced 75 cm apart, with seeds planted 25 cm apart in each row to give a 40-plant population per plot. A week before planting, all experimental plots were amended with 5 t/ha cow manure. Basal side dressing fertilizers consisting of 100 kg/ha Urea, 150 kg/ha SP36, and 100 kg/ha KCl were applied one week after planting, and an additional 100 kg/ha of Urea

was applied as the plant population reached the silking stage. Insect pests, diseases, and weeds were well controlled. Ears were harvested as the kernel reached the early dough stage.

Data collection and analysis

The meteorological data were gathered using automatic weather stations set up in each location. The phenological stages were determined as the number of days after sowing (DAS) required by $\geq 50\%$ of plants from each plot to attain the following stages: emergence (VE), third leaf (V3), fifth leaf (V5), tenth leaf (V10), tasseling (VT), silking (R1), blistering (R2), milk (R3), and dough (R4) stages, as described by Nleya et al. (2016).

Growing degree days (GDD) were determined for each phenological stage of plants beginning with crop emergence through dough using the following formula (McMaster and Wilhelm, 1997):

$$\text{GDD (}^{\circ}\text{C days)} = \sum \left[\left(\frac{T_{\max} + T_{\min}}{2} \right) - T_{\text{base}} \right] \quad (1)$$

where T_{\max} and T_{\min} are the recorded maximum and minimum daily temperatures, respectively. T_{base} is the base temperature of 10°C , which was used as the minimum temperature for sweet corn growth.

Both green ear yield (GEY) representing the weight of marketable unhusked ears, and biological yield (BioY) representing the total weight of roots, stalks, leaves, and ears based on the population density of 53000 plants/ha, were recorded at harvest in t/ha. The harvest index of marketable ears (HI) was determined as the percentage of GEY to BioY as follows (Ludemann et al. 2022):

$$\text{HI} = \frac{\text{GEY}}{\text{BioY}} \times 100\% \quad (2)$$

Heat use efficiency (HUE) was determined as the ratio of GEY to GDD at harvest (R4) as follows (Jan et al. 2022):

$$\text{HUE (kg/ha) /}^{\circ}\text{C d)} = \frac{\text{GEY}}{\text{GDD}} \quad (3)$$

The collected data were subjected to a combined analysis of variance (Steel and Torrie, 1980), and the means were compared using the Least Significant Difference (LSD) at $\alpha = 0.05$. The normality of the error distribution was confirmed by the Shapiro-Wilk test before performing the analysis of variance. The analysis was performed using PROC GLM in SAS version 9.4 (SAS Institute Inc., Cary, NC).

Conclusion

While the inherent air temperatures in the humid tropics fall within the range of optimum temperatures for sweet corn growing, cooler temperatures at higher elevations will allow the plants to grow longer with fewer growing degree-days, resulting in increased photosynthate production for both ear yield and biological yield improvement with higher heat use efficiency. By being in the same maturity group, the sweet corn hybrids had similar responses to changes in elevational temperature based on their phenological stages and growing degree day needs, but not in how they made and used photosynthate or heat use efficiency.

Acknowledgement

We would like to express our gratitude to the University of Bengkulu for providing financial support toward this research project (Grant number: 1758/UN30.15/PG/2021).

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