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Relationship between Photosynthetic Rate and Stomatal Conductance, Intercellular CO₂ Concentration, Transpiration Rate, Vapour Pressure Deficit and Photosynthetically Active Radiation in Sweet Corn (*Zea mays*)

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Abstract: Sweet corn (Zea mays) is the third-largest plantation crop in Malaysia. Since it is cultivated mainly for the corncobs, the reproductive and kernel development stages are critical for high yields. Photosynthesis measurement can be used as a major approach to improve photosynthetic efficiency, which can directly affect yield. Additionally, plant nutrient uptake also plays a major role in yield quantity and quality. Conventional fertilisation (chemical and/or organic) may result in excessive fertilizer input, which is detrimental to the environment. We therefore investigated the relationship between photosynthetic rate and stomatal conductance (g_s), intercellular CO₂ concentration (Ci), transpiration rate and vapour pressure deficit based on leaf temperature (VpdL) and photosynthetically active radiation (PAR) during the growth and development stages of sweet corn. The seeds were subjected to the germination test to assess viability and were then planted at a distance of 10 cm both between plants and rows (replicates). A total of eight subplots (2.2 m long, 60 cm wide, 30 cm high) were prepared in a randomized complete block design (RCBD). Leaf gas exchange measurements were carried out at days 10, 20, 30, 40, 50 and 60 at 9:00 a.m. in the morning and 4:00 p.m. in the evening. Three uniform plants were selected from each replicate and used for measurements throughout the experiment. At day 30, photosynthesis started to decline and was largely unaffected by the set environmental conditions, although stomatal conductance remained high. This can be attributed to the energy diversion from vegetative stages to reproductive stages. Therefore, fertilising practices should be synchronised to match the plant stages for more sustainable and efficient fertilisation and to obtain maximum yield.

Keywords: Photosynthesis rate, stomatal conductance, intercellular CO₂ concentration, transpiration rate and leaf temperature

1. Introduction

In 2017, Malaysia produced 1.7 million tons of corns, and the production is increasing [1]. Sweet corn (*Zea mays*) cultivation takes about 65-72 days, and in the relatively short growth period, photosynthesis is a critical factor, similar to numerous other autotrophic plants. Via photosynthesis, plants synthesise nutrients from carbon dioxide and water [2].

Fertiliser inputs is one of the most significant agronomic practices in sweet corn cultivation, with the aim to improve soil fertility and increase crop productivity [3]. Nitrogen (N) is one of the most important nutrients and crucial for optimum growth and yield. Similarly, phosphorus (K) is needed for enhanced root development, consequently increasing vegetative growth and yield [4]. Currently, fertiliser input levels are based on soil fertility and plant morphology, mostly neglecting plant physiology, particularly photosynthesis. This may lead to an excessive use of fertilisers, which may be detrimental to the environment especially due to leaching [5]. Stomatal pores on the leaf surface regulate the intercellular carbon dioxide (CO₂) concentration (C_i) during photosynthesis, also allowing water vapour to leave the plant via transpiration; under water limitation, they close to avoid dehydration. The capacity of stomata to control gas exchange and water vapour between the leaf and the external environment is known as stomatal conductance (g_s) [6]. Photosynthetic response can be strongly related to g_s , which is generally triggered by CO₂ level, vapour pressure deficit (VPD), temperature and photosynthetically active radiation (PAR) [7]. However, one other, often overlooked variable is the plant growth stage, namely vegetative and reproductive stages.

The main objective of this study was to understand plant physiological changes in relation to photosynthesis. Specifically, this study was conducted to determine the relation between photosynthetic rate and g_s, C_i, transpiration rate and vapour pressure deficit based on leaf temperature (VpdL) and PAR during the growth and development of sweet corn.

2. Materials and Method

2.1 Seed Selection and Germination Test

The sweet corn hybrid Sugar King F1 (516, Leckat, Taiwan) was used and subjected to a modified seed germination test based on a previous report [8] to determine its viability. The germination test was conducted in the Soil Health Laboratory, Universiti Teknologi Malaysia (UTM), Pagoh. The seeds were arranged randomly on paper towels soaked with 5 mL of soil extract from the experimental plot; the paper towels were placed in petri dishes. There were 10 petri dishes, each containing 10 seeds. The seeds were then incubated in the dark at $23 \pm 2^{\circ}$ C for 3 days, and after this, the number of germinated seeds was determined and radicle growth was analysed at day 3. A 90% seed germination index was obtained from relative seed germination and relative radicle growth.

2.2 Field Experiment

The field experiment was conducted on the Research Farm Plot in UTM Pagoh, Johor. The soil was moderately coarse sandy loam with a pH of 5.5-6.0. The 300-m² plot was prepared by conventional tractor ploughing and rotary tilling in 14-day intervals. A disc ridge was used to prepare the planting beds prior to the experiment.

2.3 Experimental Treatments and Design

The seeds were planted at a distance of 10 cm both between plants and rows. In total, eight subplots with a length of 2.2 m, a width of 60 cm and a height of 30 cm were prepared in a randomised complete block design (RCBD) (Fig. 1) [9]. There were 10 plants per row (10 x 10 cm) and 3 rows (30 plants in total) per subplot, of which each row represented one replicate (Fig. 2). Burned rice husk was applied before planting at a rate of 5 t/ha. Bio-organic compound fertiliser (5:5:5) was applied during planting at a rate of 200 kg/ha and further (15:15:6:4) at days 15 and 40 at a rate of 200 kg/ha [10]. Plants were grown without pesticides and herbicides, but with insect repellent and manual weeding. Irrigating was performed twice a day except when raining.

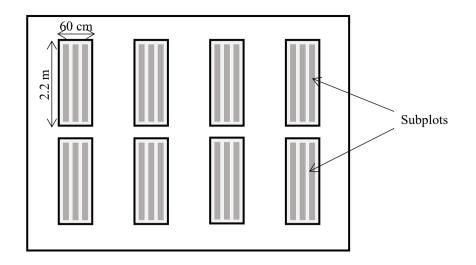


Fig. 1 - General layout of the experiment with eight subplots arranged in a randomised complete block design (RCBD).

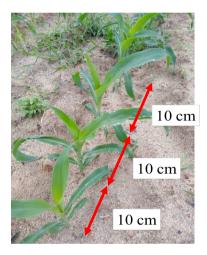


Fig. 2 - Sweet corn (Zea Mays) was planted in a plot with a distance of 10 x 10 cm.

2.4 Leaf Gas Exchange Measurements

Gas exchange was measured using an LI-6400XT portable photosynthesis system with a 6400-02B LED light source (Li-Cor Inc., USA) (Fig. 3). The environmental conditions were set at 1,500 μ mol m⁻²s⁻¹ quantum flux, 400 μ mol s⁻¹ airflow and 400 μ mol mol⁻¹ reference CO₂, while the temperature was not set. These conditions were selected to mimic field conditions. Measurements were taken at days 10, 20, 30, 40, 50 and 60 at 9:00 a.m. in the morning and 4:00 p.m. in the evening. Three uniform plants in each replicate were selected and clamped for the experiment [11]. Data were manually logged only when all the set parameters were stable.



Fig. 3 - Picture showing the leaf gas exchange measurement with the 6400-02B LED light source.

2.5 Statistical Analysis

Data from the gas exchange measurements of g_s, C_i, transpiration rates, VpdL and PAR were averaged and analysed using two-way analysis of variance (ANOVA) to assess the effects of measured parameters on photosynthetic rates. The analysis was performed with IBM SPSS Statistics version 22 (IBM Corp., Armonk, NY). Pearson's correlation coefficient was used to evaluate the linear association between the measured parameters at the 5% significance level.

3. Result and Discussion

Figure 4 shows the relation between g_s and photosynthetic rate. All readings indicated higher g_s values and photosynthetic rates in the morning compared to the evening, except at day 60. There was a significant relation between morning g_s and photosynthetic rates up to day 30 (p < 0.05); the relation was insignificant (p > 0.05) from day 40 onwards. However, there was a significant positive relation between evening g_s and photosynthetic rates throughout the experiment (p < 0.05). The highest morning g_s readings were between 0.60 and 0.80 mol H₂O m⁻² s⁻¹ from days 40 and 60, while the highest photosynthetic rate occurred at day 30 in the evening, reaching 1.50 µmol CO₂ m⁻² s⁻¹. The g_s corresponded significantly to various factors including VPD and PAR up to day 30, after which this relation seemed insignificant, suggesting another factor may also have played a role in g_s . Additionally, the sensitivity of g_s may have reduced at the later stages of the plant growth. Therefore, it is recommended to apply fertilisers in the morning up until day 30, after which and specifically N fertilizers which generally directly correspond to photosynthesis did not occur [12] [13].

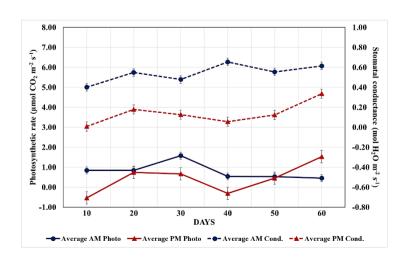


Fig. 4 - Photosynthetic rate versus stomatal conductance in sweet corn.

Figure 5 shows the relation between C_i and photosynthetic rate. The C_i was relatively erratic up to day 30, suggesting that immature stomatal development may have played a role. After this, C_i began to show a more representative coordination with the VPD, mainly at day 40 and beyond. A reduced VPD increases biomass, in particular at the leaf area, which may also increase the stomatal count from increased organic matter. This was shown from the highest C_i of 14.00 µmol CO₂ mol⁻¹ at day 40. A subsequent reduction in C_i indicates the deterioration of stomatal cells, as the plant was approaching the end of its life cycle. The photosynthetic rate was also highest at 1.50 µmol CO₂ m⁻² s⁻¹ at day 30, when the C_i was the lowest. Based on previous studies, in the morning, the conditions for CO₂ to diffuse into the leaves are more conducive [14] [15]. However, most likely, the low photosynthetic rates, despite the high Ci values, were due to decreased stomatal sensitivity to CO₂ in the later stages of growth.

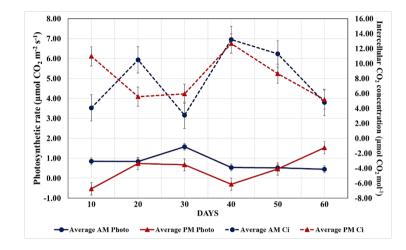


Fig. 5 - Photosynthetic rate versus intercellular CO₂ concentration in sweet corn.

Figure 6 shows the relation between transpiration rate and photosynthetic rate. There was a positive significant relation between evening transpiration rates and photosynthetic rates (p < 0.05), while there was no significant relation for both morning rates (p > 0.05). The morning transpiration rates were always higher than those in the evening, except at day 60. This was significantly correlated to the g_s value, where the higher VPD and temperature values in the evening triggered stomatal closure to maintain the water balance and to avoid excessive transpiration [16] [17]. These reduced transpiration rates were also crucial in reducing the effect of turgor loss under high evaporation demand to balance the insufficient water flux in the plants. The highest transpiration rate obtained was 12.00 mmol H₂O m⁻²s⁻¹ at day 40, most likely as a result of partial stomatal closure following a triggered opening prior to the measurements.

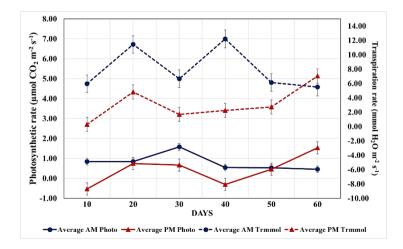


Fig. 6 - Photosynthetic rate versus transpiration rate in sweet corn.

Figure 7 shows the relation between VpdL and photosynthetic rate. The VpdL readings in the morning were always lower than those in the evening, indicating lower ambient temperature [18] [19]. There was no significant relationship between VpdL and photosynthetic rates (p > 0.05). Lower VpdL values triggered stomatal opening, resulting in higher photosynthetic rates. Additionally, the reduced VpdL resulted in increased relative water content (RWC) and higher leaf water potential (ψ_{leaf}). This, in turn, maintained the high leaf water status, which also benefitted CO₂ diffusion through the stomata. The highest VpdL reading was 3.00 kPa at day 30. Lower VpdL values at day 40 and beyond indicate a maintained high water content and water potential despite the relatively high transpiration rate. This might be due to heavy rain, which resulted in high soil water content to compensate the balance between plant water status and evaporative demand.

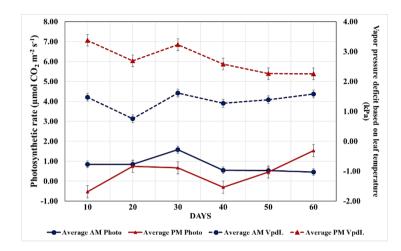


Fig. 7 - Photosynthetic rate versus vapour pressure deficit in sweet corn, based on leaf temperature.

Figure 8 shows the relation between PAR and photosynthetic rate. There was no significant relationship between PAR and photosynthesis rate (p > 0.05). This was also evidenced by the relatively low photosynthetic rate, even at the highest PAR at 1,340 µmol m⁻² s⁻¹ at day 20. Light irradiance promotes stomatal opening; however, in our study, this was not the main factor affecting photosynthesis. By extension, stomatal opening was independent of PAR exposure, although the impact of PAR on photosynthesis has been reported previously [20] [21]. Additionally, PAR use efficiency depends on the stages of plant growth (vegetative versus reproductive), which was also found in this experiment.

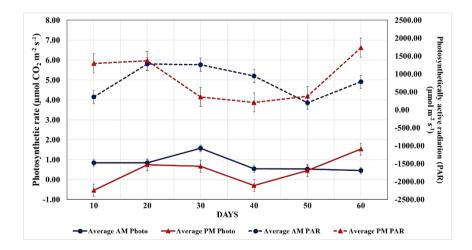


Fig. 8 - Photosynthetic rate versus photosynthetically active radiation in sweet corn.

4. Conclusions

At day 30, photosynthesis started to decline and was largely unaffected by the environmental conditions normally associated with photosynthesis, although stomatal conductance remained high. This can be attributed to the energy diversion from vegetative to reproductive stages. Therefore, fertilising practices should be synchronised to match the plant stages in addition to the nutrient requirement for more sustainable and efficient fertilisation, resulting in maximum yield and higher economic efficiency. The results of this study can be applied to other crops and used to develop sustainable agricultural practices without compromising food security.

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