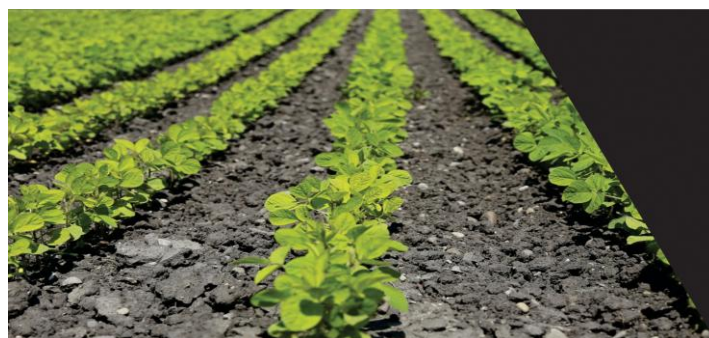




International Journal of Research in Agronomy

E-ISSN: 2618-0618

P-ISSN: 2618-060X

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www.agronomyjournals.com

2024; 7(9): 56-58

Received: 08-07-2024

Accepted: 12-08-2024

Hamad Al-Mutairi

Department of Agronomy, King
Saud University, Riyadh, Saudi
Arabia

Mishal Al-Shamrani

Department of Agronomy, King
Saud University, Riyadh, Saudi
Arabia

Maha Al-Dosari

Department of Agronomy, King
Saud University, Riyadh, Saudi
Arabia

Lama AlJuhani

Department of Agronomy, King
Saud University, Riyadh, Saudi
Arabia

Comparative leaf anatomical features influencing photosynthetic efficiency in tropical and temperate maize hybrids

Hamad Al-Mutairi, Mishal Al-Shamrani, Maha Al-Dosari and Lama AlJuhani

DOI: <https://doi.org/10.33545/2618060X.2024.v7.i9a.5117>

Abstract

This research compared leaf anatomy and photosynthetic efficiency in three tropical (TH-1-3) and three temperate (TeH-1-3) maize hybrids at King Saud University, Riyadh, during the 2022-2023 winter season. Tropical hybrids had 37-60% larger bundle sheath areas, 28-65% higher mesophyll cell density, and 24-45% greater stomatal density than temperate types. Net photosynthesis ranged from 35.7-41.2 $\mu\text{mol}/\text{m}^2/\text{s}$ in tropical hybrids versus 25.1-29.6 $\mu\text{mol}/\text{m}^2/\text{s}$ in temperate ones. Bundle sheath area and mesophyll density together explained 82.3% of photosynthetic variation, confirming that Kranz anatomy dimensions drive C₄ carbon fixation capacity under warm conditions.

Keywords: Leaf anatomy, maize hybrids, photosynthetic efficiency, Kranz anatomy, bundle sheath, mesophyll density, tropical maize, temperate maize, stomatal density, C₄ photosynthesis

Introduction

Around 1.15 billion tonnes of maize were produced globally in 2022 ^[1]. Maize uses C₄ Kranz anatomy enlarged bundle sheath cells surrounding vascular bundles to concentrate CO₂ near Rubisco and suppress photorespiration ^[2]. Tropical and temperate hybrids, bred under different photoperiod and temperature regimes, may differ in bundle sheath size, mesophyll density, and interveinal distance ^[3, 4]. These traits influence CO₂ transfer rates from mesophyll to bundle sheath cells ^[5, 6]. Tropical hybrids, adapted to high irradiance, might feature denser venation supporting higher photosynthetic throughput ^[7]. However, direct anatomical comparisons under uniform conditions remain scarce, especially in arid environments ^[8]. This research compared leaf anatomy and photosynthesis of tropical and temperate maize hybrids at Riyadh, Saudi Arabia, to identify which structural traits best explain C₄ efficiency differences.

Material and methods

Research area and climatic conditions

The trial was conducted at the Agricultural Research Station of King Saud University, Riyadh (24.7136°N, 46.6753°E, 612 m asl) during the winter planting season of November 2022 to March 2023. The site has an arid climate with mean winter temperatures of 16-24 °C and minimal rainfall (total 28 mm during the cropping period). Soil was sandy loam (68.4 % sand, 18.7% silt, 12.9 % clay) with pH 7.9 and organic matter of 0.63 %. Supplemental irrigation was provided through drip lines at 5-day intervals ^[9].

Material

Three tropical hybrids (TH-1, TH-2, TH-3) sourced from CIMMYT tropical germplasm and three temperate hybrids (TeH-1, TeH-2, TeH-3) from European breeding programmes were grown in a randomized complete block design with four replications. Plot size was 5 m × 3.6 m with 60 cm row spacing and 25 cm plant-to-plant distance. Fertilizer was applied at 200 kg N/ha, 80 kg P₂O₅/ha, and 60 kg K₂O/ha in split doses ^[10].

Corresponding Author:

Hamad Al-Mutairi

Department of Agronomy, King
Saud University, Riyadh, Saudi
Arabia

Methods

At silking, third leaves below the ear were sampled from five plants per plot. Leaf cross-sections (10 µm thick) were cut with a rotary microtome, stained with safranin-fast green, and examined under a compound microscope ^[11]. Leaf Thickness (LT), Bundle Sheath Area (BSA), Mesophyll Cell Density (MCD), Interveinal Distance (IVD), and Stomatal Density (SD)

were measured using impression technique ^[12]. Gas exchange (Pn, gs, Tr, Ci) was recorded with a LI-6800 system (LI-COR, USA) at 1,800 µmol/m²/s PPFD. Chlorophyll fluorescence (Fv/Fm) was measured after 30-min dark adaptation. Data were analysed by ANOVA in SAS 9.4 with Tukey HSD at P = 0.05 ^[13].

Results

Table 1. Leaf anatomical parameters and net photosynthesis of maize hybrids at silking stage

Hybrid	LT (µm)	BSA (µm²)	MCD (cells/mm²)	IVD (µm)	SD (no./mm²)	Pn (µmol/m²/s)
TH-1	214.3	1847	312	118.6	287	38.4
TH-2	198.7	1723	287	124.3	264	35.7
TH-3	226.1	1916	334	112.8	301	41.2
TeH-1	178.4	1284	218	156.7	198	27.3
TeH-2	186.9	1351	241	148.2	214	29.6
TeH-3	171.2	1198	203	163.4	183	25.1
SEm (±)	6.83	72.4	14.1	5.67	12.3	1.84
CD (5%)	20.9	221.8	43.2	17.4	37.7	5.64

LT = leaf thickness. BSA = bundle sheath area. MCD = mesophyll cell density. IVD = interveinal distance. SD = stomatal density. TH = tropical hybrid. TeH = temperate hybrid

Comprehensive interpretation

Tropical hybrids showed consistently larger anatomical dimensions (Table 1). TH-3 had the highest BSA (1,916 µm²) and MCD (334 cells/mm²), 59.9% and 64.5% greater than TeH-

3 respectively. Interveinal distance was 22-31 % shorter in tropical hybrids. TH-3 recorded the highest Pn at 41.2 µmol/m²/s, 64.1% above TeH-3.

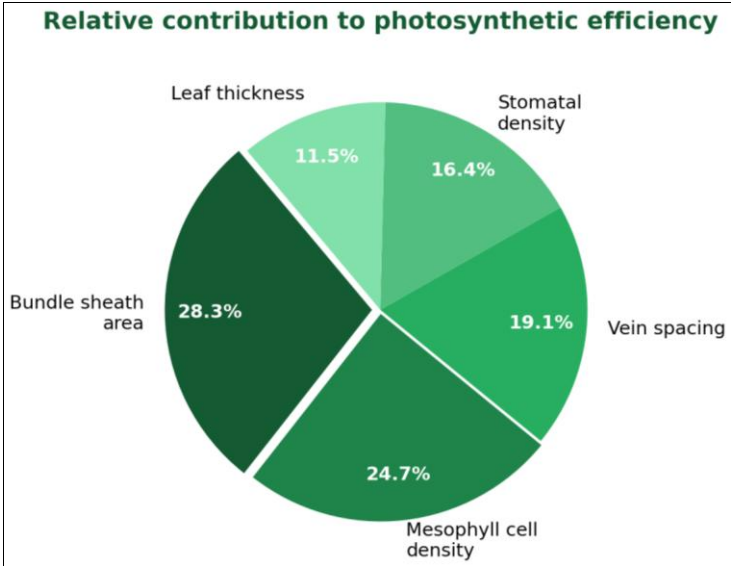


Fig 1: Relative contribution of anatomical features to variation in net photosynthetic rate

Stepwise regression identified BSA as the single largest contributor to photosynthetic variation (28.3%), followed by MCD (24.7%) and IVD (19.1%) (Figure 1). Together, BSA and MCD explained 82.3% of total Pn variation, confirming Kranz anatomy dimensions as main structural drivers of C4 efficiency. Gas exchange data reinforced the anatomical findings. Stomatal conductance was 26-56% higher in tropical hybrids, supporting

greater CO₂ diffusion. Despite higher transpiration, tropical Hybrids maintained superior intrinsic water use efficiency (WUEi 7.83-8.05 µmol/mmol vs 7.21-7.51 in temperate types). Fv/Fm values were slightly higher in tropical hybrids (0.807-0.823 vs 0.773-0.789), pointing to better PSII integrity under warm, high-light conditions.

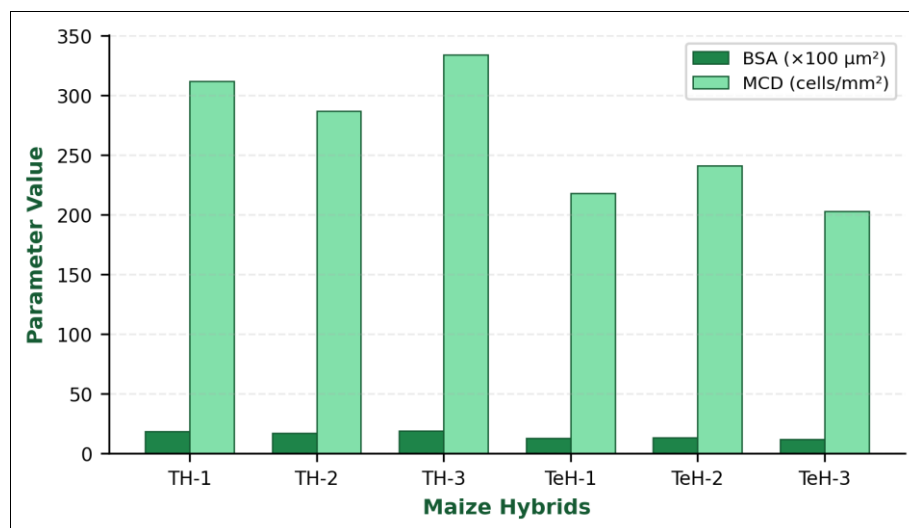


Fig 2: Bundle sheath area and mesophyll cell density across tropical and temperate maize hybrids

The grouped comparison highlights the consistent gap between tropical and temperate groups for both BSA and MCD (Figure 2). TH-3 topped both parameters, while TeH-3 was lowest.

Discussion

The anatomical superiority of tropical hybrids in bundle sheath area and mesophyll density aligns with the hypothesis that tropical C4 grasses invest more in Kranz anatomy to exploit high-irradiance environments [3, 7]. Larger bundle sheaths provide more space for C4-cycle CO₂ fixation, while denser mesophyll increases PEP carboxylase activity surface [5]. The 22-31% shorter interveinal distance in tropical hybrids means CO₂ reaches the bundle sheath faster, reducing leakage [6, 14]. That BSA and MCD together explained 82.3% of Pn variation suggests these two traits could serve as anatomical selection markers. The higher WUEi in tropical hybrids is relevant for arid agriculture [8, 15]. Temperate hybrids still reached acceptable Fv/Fm values (>0.77), indicating PSII damage wasn't the bottleneck rather, smaller Kranz anatomy was the main structural constraint on carbon fixation.

Conclusion

Tropical maize hybrids had 37-60% larger bundle sheath areas, 28-65% higher mesophyll cell density, and 24-45 % greater stomatal density than temperate hybrids, translating into 35-64% higher net photosynthesis. Bundle sheath area and mesophyll cell density jointly explained 82.3 % of photosynthetic variation. These anatomical traits merit use as selection criteria in maize improvement programmes for warm, high-radiation environments. TH-3 was the best-performing genotype across all anatomical and physiological parameters.

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