

WEATHER FACTORS AFFECTING CANOPY ORIENTATION OF MAIZE IN THE RAINFOREST OF SOUTHWESTERN NIGERIA

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DOI: <https://doi.org/10.51193/IJAER.2022.8303>

Received: 14 May 2022 / Accepted: 28 May 2022 / Published: 22 Jun. 2022

ABSTRACT

Despite the wide recognition of plant architecture as a key factor for optimum productivity in most crops, factors affecting maize (*Zea mays* L.) crop configuration is poorly understood and often neglected in the rainforest ecologies of sub-Saharan Africa. The present study provides an analysis of the weather factors affecting canopy architecture of maize in the rainforest of sw Nigeria. Five maize varieties were planted weekly from March to November of 2016 and 2017 in randomized complete block experiments at the Obafemi Awolowo University Teaching & Research Farm (OAU T&RF). Data were collected on upper and lower leaf angle (LA_{Upper} and LA_{Lower}), and leaf orientation values (LOV_{Upper} and LOV_{Lower}) which served as indices for canopy architecture. Weather data were obtained from the automatic weather station located on the farm. ANOVA revealed that environment had significant effects on canopy architecture and grain yield ($P = 0.01$; $R^2 \geq 80\%$). Correlation and regression analyses showed that soil moisture, soil temperature, and solar radiation greatly affected canopy configuration ($P \leq 0.01$), particularly LA and LOV. Sequential path analyses confirmed that soil moisture for LA, and soil temperature for LOV, were the most important weather factors directly influencing canopy architecture in maize. Leaf angle was directly influenced by soil moisture and indirectly by air relative humidity and rainfall, while LOV was directly influenced by soil temperature and solar radiation, and indirectly by air relative humidity, heat unit, total radiation, rainfall, and soil heat flux.

Keywords: Climatology, crop physiology, leaf angle, leaf orientation value, phenology, *Zea mays* L..

1. INTRODUCTION

The importance of maize in the economy and diets of the populations of sub-Saharan Africa (SSA) cannot be overemphasized and has been discussed extensively in the literature (Talabi *et al.*, 2017; Fayose *et al.*, 2022). The general factors that affect maize growth have also been well covered by previous studies to include biotic and abiotic factors (Fakorede *et al.*, 2003; Khan *et al.*, 2006). In the past decades, climatic effect on many aspects of crop growth and development has become prominent due to climate change which has often manifested in varying impacts on different crops, depending on location and time. The impact of climate change on crops has intensified in recent times. Fakorede and Akinyemiju (2003) reported a progressive reduction in the effective growing season at the Obafemi Awolowo University Teaching and Research Farm (OAU T&RF) for three decades, from about 1975 to 2000 due to climate change, a trend that has intensified in recent times (Fayose and Fakorede, 2021a). Regrettably, the relationship between climate and different aspects of growth and development for most tropical crops is poorly understood as a result of the little research attention given to it hitherto. Despite the wide recognition of plant architecture as a key factor for optimum productivity in most crops, canopy architecture and its relationship with weather factors in maize has received little attention from researcher in SSA, a trend that must be urgently addressed if we are to cope with the impacts of climate change on maize production. The leaf plays a major role in plant nutrition through photosynthesis and other physiological functions. Several studies have established a relationship between different aspects of leaf canopy architecture and maize productivity, grain yield in particular (Pepper *et al.*, 1977; Vazin *et al.*, 2010; Li *et al.*, 2015; Huang *et al.*, 2017). Most of the authors used leaf angle (LA) and leaf orientation value (LOV) as indices to establish the relationship of canopy architecture with grain yield. Pepper *et al.* (1977) observed yield advantages for genotypes with lower LOV when leaf area indices were high. Li *et al.* (2015) found significant effect of genotype on leaf parameters including LOV, and grain yield in recombinant inbred lines (RIL). Huang *et al.* (2017) observed a significant reduction in grain yield and its components of plants where leaf orientation was modified compared to the unmodified plants. Studies by Ku *et al.* (2010) and Vazin *et al.* (2010) also recognised a relationship of canopy architecture cum leaf health with some variables of climate, especially solar radiation. They found that canopies with reduced exposure to solar radiation exhibited early senescence. Similarly, Duvick (2005) noted that optimum leaf configuration would improve maize grain yield by enhancing light capture for photosynthesis, serving as nitrogen reservoirs for grain filling, enabling denser planting with a higher leaf area index and reducing premature

leaf senescence. Unfortunately, there is paucity of information on the role of other weather variables that influence this important aspect of crop growth beyond solar radiation and light.

It is necessary to test the hypotheses that (i) there is no relationship between weather factors and canopy architecture; and (ii) genotype and environment do not influence maize canopy architecture. Results of such studies would facilitate a better understanding of the response of maize to weather factors and ensure better adaptation of maize to environments, where climate change effects will be minimal in order to boost yield output.

The objectives of the study reported here were to (i) identify the weather factors responsible for the expression of different canopy architecture traits and (ii) determine whether there were significant genotypic, environmental, and genotype x weather factor interaction effects on maize canopy architecture.

2. MATERIALS AND METHODS

2.1. Experimental location, design and planting material

The study was carried out at the Teaching and Research Farm of Obafemi Awolowo University, Ile-Ife (OAU T&RF) in years 2016 and 2017. The environmental features of the OAU T&RF and details of experimental design and planting materials have been reported earlier (Fayose and Fakorede, 2021a; Fayose *et al.*, 2022), therefore only relevant information are presented here. In each experiment, five maize varieties (four OPVs and one single-cross hybrid), fully adapted to the tropical rainforest environments, were planted in 3-replicate randomized complete block designs. The experiments were planted weekly (environment) from March to November each year; 56 environments (28 each year) were planted, out of which 42 environments (20 in 2016 and 22 in 2017) attained maturity and were analyzed for leaf angle and grain yield along with its components; 39 environments were analyzed for leaf orientation value. Each plot contained six or four rows which were 5 m long and 0.75 m apart; within row spacing was 0.5 m and plot size was 15 m² and 22.5 m² for the four and six-row plots, respectively. Three seeds were planted per hill and thinning was done at 9 days after planting (DAP) to two plants per stand giving an estimated plant population density of 53,333 plants ha⁻¹. Necessary agronomic practices were done before and after planting as described in the previous studies cited above.

2.2. Data collection

Data were collected on leaf angle (LA_{Upper} and LA_{Lower}) and orientation (LOV_{Upper} and LOV_{Lower}) for the upper and lower leaves (see Fayose *et al.*, 2022 for details). Data were also collected on grain yield and yield components (ear length, ear diameter, and kernel row number). The grain yield data were adjusted to 15% moisture content.

Minimum and maximum air temperatures and relative humidity (RH), rainfall, soil moisture (Sm), solar radiation, net radiation, wind speed, soil temperature at 2cm, 5 cm, 10cm, 20cm and 50cm for Ts 1, 2, 3, 4 and 5; respectively, and soil heat flux were monitored from the automatic weather station (AWS), OAU MET Station, of the Atmospheric Physics Research Group located on the OAU T&RF. The experimental plots were within 100 – 500 meters of the weather station mostly in plain sight except for the last four environments in 2016 that had a slightly dense vegetation inbetween. Weather tracking sensors at the station are as described by Fayose and Fakorede (2021a). Heat unit was computed from the minimum and maximum temperature per day as given below:

$$HU = \sum_{i=1}^n \left(\frac{X_i^H + X_i^L}{2} \right) 10$$

where X_i^L is the minimum temperature for the day ($^{\circ}\text{C}$), X_i^H is the maximum temperature for the day ($^{\circ}\text{C}$) ($X_i^H = 30$ if $X_i^H > 30^{\circ}\text{C}$, $X_i^H = X_i^H$ if $X_i^H \leq 30^{\circ}\text{C}$), and 10°C is the base temperature (Abasi *et al.*, 1985).

2.3. Statistical analysis

Variance analysis for a mixed model was done on all data using PROC GLMM of Statistical Analysis System (SAS, 2000) as detailed by Fayose *et al.* (2022). Furthermore, correlation, stepwise multiple regression, and sequential path analyses were done for all data as explained by Fayose and Fakorede (2021a), to determine the relationship of canopy architecture indices with maize grain yield and climatic variables. The stepwise multiple regression analysis was done using the Statistical Package for Social Sciences (SPSS Inc, 2007) to provide information on the path coefficients and the causal relationships required for the path diagrams. The predictor variables, in this case, were the weather factors. They were organized into first, second, and third order, based on their contributions to the total variation in the predicted traits (leaf architecture indices) with minimized multicollinearity. To perform the stepwise regression analysis, each leaf architecture index was regressed on all the climatic variables to identify those with significant contributions to the variation in the leaf architecture traits at $P \leq 0.05$, and they were categorized as first order variables. The first-order variables thereafter were each regressed on other climatic variables which were not in the first order category, to identify the climatic variables with significant contributions to the leaf architecture traits through the first-order variables. These variables were classified as second order variables. The procedure was repeated to identify third order variable(s) and so on. The path coefficients were obtained from the standardized b-values of the stepwise multiple regression analysis and were tested for significance using the standard

errors at 0.05 probability level. Only traits having significant path coefficients were retained in the path diagram.

3. RESULTS

Details of results from the variance analysis is contained in earlier report by Fayose *et al.* (2022), where highly significant environmental (E) and varietal (V) effects were observed for all leaf architecture indices and grain yield along with its components. Attention here is on the effect of weather factors on maize canopy architecture response to environment.

The upper (LOV_{Upper}) and lower (LOV_{Lower}) LOV increased with increased soil temperature, average radiation, and total global radiation but decreased with increased minimum air relative humidity (RH) at $P \leq 0.01$ (Table 1). Soil moisture (Sm) also tends to decrease LOV_{Lower} but had no effect on the LOV_{Upper} . However, both upper and lower leaf angle (LA_{Upper} and LA_{Lower}) decreased with increased Sm. Air temperature variables also increased LA_{Lower} but it decreased with mean air RH. All soil temperature levels except at 2 cm depth (Level 1) increased LA_{Upper} but not mean and maximum air RH ($P \leq 0.05$). Stepwise multiple regression, followed by simple linear regression, showed that Sm had effects on LA_{Upper} and LA_{Lower} but with quite low R^2 values [$\hat{Y} = 38.80 - 66.55X$ ($R^2 = 0.19$) and $\hat{Y} = 32.80 - 61.91X$ ($R^2 = 0.21$) for LA_{Upper} and LA_{Lower} , respectively]. Soil temperature (X_1) and average global radiation (X_2) were the climatic variables that significantly influenced LOV_{Upper} with higher R^2 value [$\hat{Y} = 6.31X_1 - 0.16X_2 - 131.04$; ($R^2 = 0.61$)] – soil temperature at 10 cm depth (Level 3) contributed 46% of the total 61% R^2 value (Table 2). Soil temperature was the only climatic variable that significantly influenced LOV_{Lower} as observed from the regression equation: $\hat{Y} = 0.96X - 11.01$; again, with a relatively low R^2 value ($R^2 = 0.38$).

Table 1: Correlation coefficients between climatic factors and leaf parameters of five maize varieties evaluated at the OAU T&R Farm in 2016 and 2017.

	LA _{Upper} [†]	LA _{Lower}	LOV _{Upper}	LOV _{Lower}
Soil temperature 1 ^ϕ	0.36	0.03	0.67**	0.60**
Soil temperature 2	0.39*	0.08	0.68**	0.61**
Soil temperature 3	0.41*	0.10	0.68**	0.62**
Soil temperature 4	0.44*	0.13	0.68**	0.63**
Soil temperature 5	0.46*	0.16	0.68**	0.64**
Soil heat flux	0.30	0.38*	0.05	0.05
Soil moisture	-0.43*	-0.46*	-0.43*	-0.42*
Rainfall	-0.18	-0.18	-0.19	-0.10
Wind speed	-0.14	-0.09	-0.06	-0.16
Mean air temperature	0.32	0.39*	0.21	0.20
Minimum temperature	0.27	0.40*	0.07	0.08
Maximum temperature	0.35	0.37*	0.32	0.27
Heat unit	0.17	0.37*	-0.02	0.08
Mean relative humidity	-0.40*	-0.41*	-0.38*	-0.35
Minimum humidity	-0.32	-0.17	-0.60**	-0.53**
Maximum humidity	-0.39*	-0.42*	-0.15	-0.13
Net radiation	0.27	0.28	0.22	0.34
Mean radiation	0.32	0.06	0.59**	0.57**
Total radiation	0.32	0.19	0.51**	0.56**

*,** - Significance at 0.05 and 0.01 level of probability, respectively

[†] LA_{Upper} = upper leaf angle in degree, LA_{Lower} = lower leaf angle in degree, LOV_{Upper} = upper leaf orientation value, LOV_{Lower} = lower leaf orientation value.

^ϕSoil temperatures at different depths (2cm, 5cm, 10 cm, 20cm and 50cm for 1, 2, 3, 4, and 5, respectively) in °C, soil heat flux in Wm⁻², soil moisture in m³/m³, rainfall in mm, wind speed in m/s, temperature in °C, relative humidity in %, solar radiation in Wm⁻², net radiation in Wm⁻².

Table 2: Regression coefficients (b-values), coefficients of determination (R^2) and changes in R^2 (ΔR^2) from the stepwise multiple regression of leaf architecture indices of five maize varieties on climatic variables at the OAU T&R Farm in 2016 and 2017.

Climatic variable	b-value	R^2	ΔR^2
	LA_{Upper}^\dagger		
Soil moisture [‡]	-66.55	0.19	0.19
	LA_{Lower}		
Soil moisture	- 61.91	0.21	0.21
	LOV_{Upper}		
Soil temperature 3	1.58	0.46	0.46
Average radiation	-0.16	0.61	0.15
	LOV_{Lower}		
Soil temperature 3	0.958	0.38	0.38

[†] LA_{Upper} = upper leaf angle in degree, LA_{Lower} = lower leaf angle in degree, LOV_{Upper} = upper leaf orientation value, LOV_{Lower} = lower leaf orientation value.

[‡]Soil temperatures at 10 cm depth in °C, soil moisture in m^3/m^3 , solar radiation in Wm^{-2} .

Sequential path coefficient analysis revealed that rainfall had a negligible indirect effect ($P = 0.115$) on LA_{Upper} via Sm, the only climatic variable that had a direct effect ($P = -0.432$) on LA_{Upper} (Figure 1). With its significantly higher path coefficient ($P = 0.908$), mean air RH was the other variable which influenced LA_{Upper} indirectly via Sm. At the tertiary level of interaction, the strong effect of net radiation ($P = 0.839$) on rainfall; and air temperature ($P = -0.22$) on mean air RH are noteworthy. Similar trend was observed for LA_{Lower} (Figure 2). The LOV_{Upper} on the other hand was significantly influenced directly by soil temperature ($P = 0.713$) and average global radiation ($P = -0.072$), but in opposite directions as indicated by the P -values, despite a strong positive correlation ($r = 0.982; P \leq 0.01$) between them (Figure 3). At the secondary level, total global radiation had a strong positive effect on mean global radiation as expected. What is strange, however, is the negative direct effect of total global radiation on soil temperature. Figure 4 revealed that rainfall again had a negligible negative effect (-0.077) on soil temperature, the only variable that had a direct causal effect on LOV_{Lower} . In contrast, average global radiation exerted a strong effect on LOV_{Lower} via soil temperature. At the tertiary level, strong positive direct effect of net radiation on rainfall is particularly conspicuous.

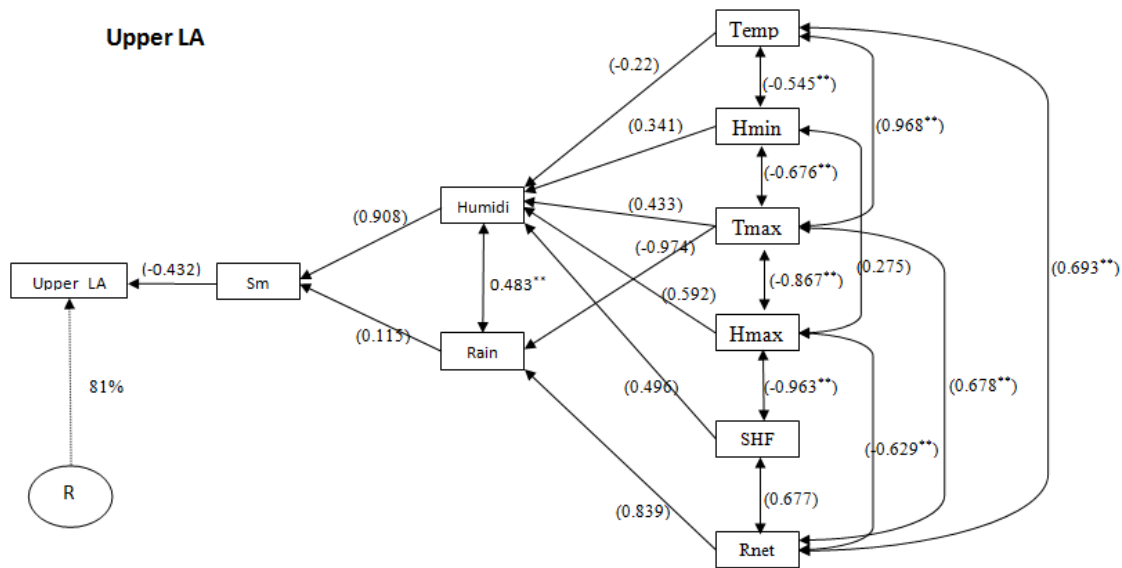


Figure 1: Sequential path-coefficient analysis diagram of climatic variables influencing the upper leaf angle. One directional arrows indicate direct effects while double arrows are correlation coefficients.

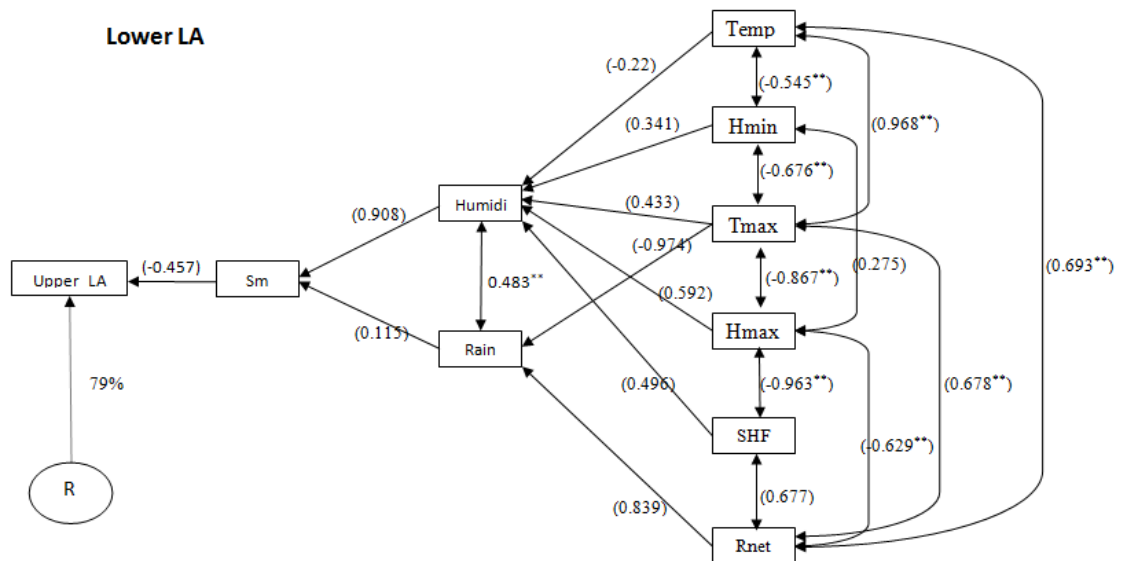


Figure 2: Sequential path-coefficient analysis diagram of climatic variables affecting the lower leaf angle. One directional arrows indicate direct effects while double arrows are correlation coefficients.

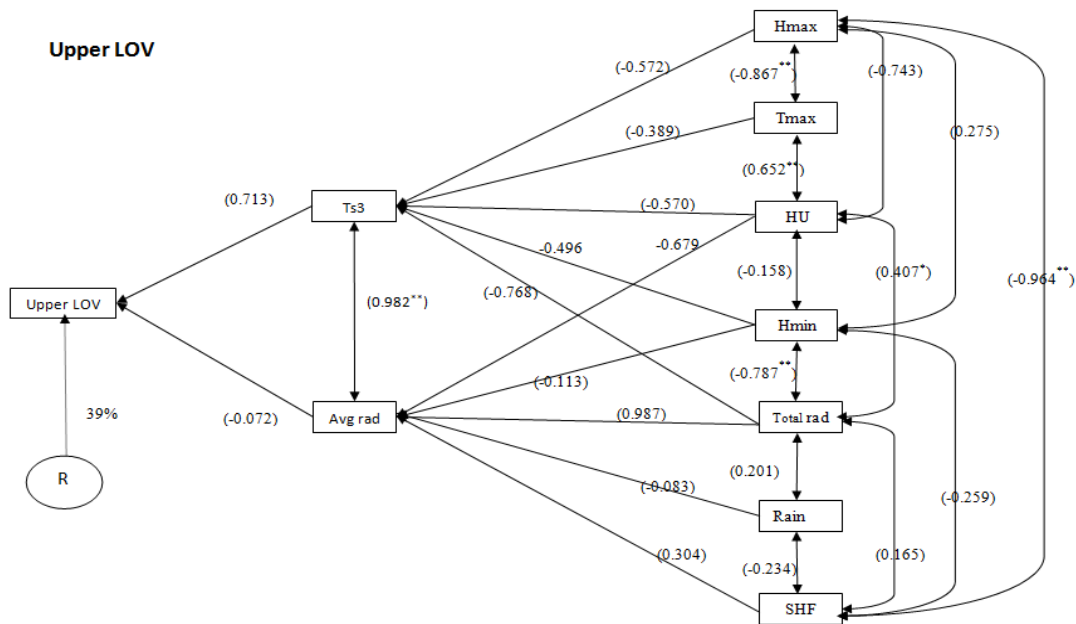


Figure 3: Sequential path-coefficient analysis diagram of climatic variables affecting the upper leaf orientation value. One directional arrows indicate direct effects while double arrows are correlation coefficients.

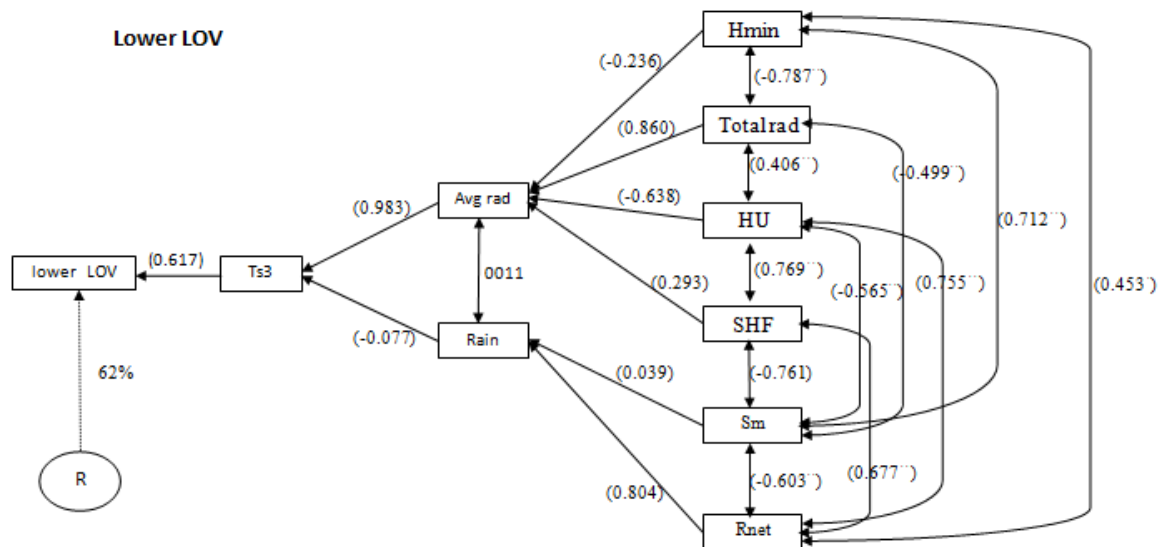


Figure 4: Sequential path-coefficient analysis diagram of climatic variables affecting the lower leaf orientation value. One directional arrows indicate direct effects while double arrows are correlation coefficients.

The upper LOV of the different varieties showed slightly different response to the climatic variables, despite its fairly consistent correlation with soil temperature (Table 3). However, LOV_{Lower} in Var 1, a hybrid, had no significant correlation with any of the climatic variables whereas the other varieties which are OPV's had different levels of correlations with the climatic variables (Table 3). Stepwise multiple regression also showed that the hybrid had no significant interaction with climatic variables. Total global radiation was the only variable that interacted significantly with LOV_{Lower} in Var 2 [$10.81 + 0.0000004X$ ($R^2 = 0.37$)]; Ts5 (X_1) and Ts4 (X_2) in Var 3 [$-38.57 + 11.27X_1 - 9.34X_2$ ($R^2 = 0.49$)]; Ts5 (X_1) and average global radiation (X_2) in Var 4 [$-78.92 + 3.84X_1 - 0.09X_2$ ($R^2 = 0.45$)]; and Ts1 in Var 5 [$-20.48 + 1.36X$ ($R^2 = 0.31$)].

Table 3: Correlation coefficients of upper and lower LOV of each of five maize varieties with climatic variables at the OAU T&R Farm in 2016 and 2017 growing seasons.

	LOV _{Upper} ^ψ					LOV _{Lower}				
	Variety 1 [†]	Variety 2	Variety 3	Variety 4	Variety 5	Variety 1	Variety 2	Variety 3	Variety 4	Variety 5
Soil temperature 1 ^φ	0.51**	0.71**	0.52**	0.34	0.65**	-0.06	0.48**	0.54**	0.52**	0.55**
Soil temperature 2	0.52**	0.72**	0.55**	0.36*	0.65**	-0.07	0.51**	0.56**	0.52**	0.52**
Soil temperature 3	0.50**	0.72**	0.55**	0.36*	0.63**	-0.07	0.53**	0.58**	0.54**	0.51**
Soil temperature 4	0.49**	0.73**	0.56**	0.39*	0.62**	-0.06	0.54**	0.61**	0.56**	0.49**
Soil temperature 5	0.47**	0.74**	0.56**	0.40*	0.60**	-0.05	0.55**	0.64**	0.57**	0.47**
Soil heat flux	-0.02	0.06	0.17	0.15	-0.15	-0.14	0.33	0.26	0.06	-0.32
Soil moisture	-0.20	-0.41*	-0.41*	-0.34	-0.36*	0.05	-0.51**	-0.45*	-0.40*	-0.15
Rainfall	-0.12	-0.11	-0.10	-0.09	-0.37*	0.02	-0.14	0.10	-0.17	-0.16
Wind speed	0.01	-0.20	-0.02	-0.04	0.05	0.05	-0.22	-0.09	-0.16	-0.12
Mean air temperature	0.07	0.22	0.28	0.22	0.09	-0.15	0.43*	0.33	0.19	-0.10
Minimum temperature	-0.05	0.08	0.17	0.16	-0.09	-0.13	0.32	0.25	0.10	-0.26
Maximum temperature	0.20	0.31	0.36	0.25	0.18	-0.17	0.48**	0.38*	0.23	-0.005
Heat unit	-0.15	0.04	0.09	0.07	-0.16	-0.15	0.38*	0.23	0.05	-0.23
Mean relative humidity	-0.22	-0.38*	-0.40*	-0.28	-0.29	0.12	-0.51**	-0.41*	-0.33	-0.07
Minimum humidity	-0.41*	-0.62**	-0.50**	-0.31	-0.60**	0.14	-0.57**	-0.45*	-0.45*	-0.47**
Maximum humidity	-0.11	-0.14	-0.24	-0.19	0.04	0.09	-0.34	-0.31	-0.15	0.26
Net radiation	0.005	0.36	0.29	0.17	0.02	-0.13	0.53**	0.55**	0.22	-0.03
Mean radiation	0.42*	0.65**	0.48**	0.30	0.56**	-0.10	0.52**	0.55**	0.46**	0.49**
Total radiation	0.27	0.60**	0.46*	0.29	0.41*	-0.13	0.61**	0.61**	0.44*	0.37*

*,** - Significant at 0.05 and 0.01 level of probability, respectively. ^ψLOV_{Upper} = upper leaf orientation value, LOV_{Lower} = lower leaf orientation value.

[†] - Variety 1 = Obasuper 1, Variety 2 = White DT STR SYN1.- TZL Comp. 1- W, Variety 3 = ACR 94 TZEComp 5C₃, Variety 4 = TZL Comp. 4 DT F₂, Variety 5 = TZL Comp. 1 C6/DT – SYN – 1 – W. ^φ- See Table 1.

4. DISCUSSION

The primary objective of this study was to investigate the response of maize canopy architecture to the climates of several environments. Results of the study revealed a highly significant environmental effect for all canopy architecture indices and grain yield. The environment alone was responsible for the largest proportion of the total variation, i.e., up to 59 % of the total sum of squares. Simply put, environment, represented by the different planting dates in 2016 and 2017 in this case, influenced the level of performance of the maize varieties used to study canopy architecture and grain yield.

It is already well known that environmental conditions vary widely from day to day at one location, and from one location to another. The edaphic, and particularly, climatic factors vary widely among locations, and account for most of the variations observed in this study. Climate has profound effects on biotic and other abiotic factors of the environment; the animals, microorganisms, and the plant types that grow in an area, and the processes leading to soil formation are all influenced by climatic factors, as a result of which its influence cannot be overemphasized (Hayward and Oguntoyinbo, 1987). In this study, climatic factors varied widely among the environments and between the two years. It could be inferred, therefore, that climatic variables played a greater role, either directly or indirectly in maize canopy architecture's response to the different environments used for the present study. The high level of correlations observed between canopy architecture indices and climatic factors further buttresses this position.

Soil moisture (Sm) appeared to be the climatic variable controlling upper and lower leaf angles, both of which had strong r -values with soil moisture. There were statistically significant, but relatively low correlation coefficients between LA_{Upper} and the different levels of soil temperature, LA_{Lower} with air RH, and LA_{Lower} with air temperature. Regression analysis confirmed that Sm had significant effects on both LA_{Upper} and LA_{Lower} but with low R^2 values. Visual observation of maize plants on the field suggested the existence of a degree of relationship between canopy architecture and moisture availability. Drought is a condition where there is very little or no water supply to the plant from the soil. An obvious symptom of drought or low soil moisture on maize plant is observed in the leaf where it folds and tends to stand erect. The direction of relationship is what might be unclear. Correlation and regression analyses suggest an inverse relationship with Sm; however, the low R^2 from regression calls for caution. More studies would need to be conducted to draw definite conclusion on this subject.

Global radiation, both average and total, had fairly strong correlations with LOV. This is not incongruous in maize physiology. Green plants depend on sunlight for food production through photosynthesis and the major site of photosynthesis is the leaf. It contains chlorophyll, a chemical substance capable of absorbing light (termed the photosynthetically active radiation, PAR), which traps the useful electromagnetic wave from the sun and uses the energy to power photosynthetic process that culminates in starch production (Campillo *et al.*, 2012). Chlorophyll gives the leaf its colour and sunlight plays an

important physiological role in the formation of 'chlorophyll a', which is a major chlorophyll type (Bewley *et al.* 2013). Furthermore, plant growth direction and general orientation is regulated by sunlight. Phototropism is an important phenomenon in living organisms especially plants that have been known to involve growth towards (positive phototropism) or away (negative phototropism) from a light source. Empirical evidences from the field suggest that maize plant exhibits positive phototropism. This is evident after lodging following a heavy rainfall when, depending on the severity of lodging, fallen plants bend at angles up to 90° towards the direction of sunlight. This process is attributed to the action of auxin, a growth hormone that moves away from the direction of sunlight, thereby promoting more rapid growth at the other side of the plant shielded from sunlight, relative to the side exposed to direct sunlight. This forces the plant to bent toward the direction of sunlight. That way, the plant is able to successfully complete its life cycle as long as there is a ball of earth around the root and other necessary growth conditions are met. Also, sunlight helps maintain an healthy leaf and prolongs their life cycle (Vazin *et al.*, 2010). The results obtained in the present study seem to corroborate the existing literature on this subject matter.

Perhaps more striking is the strong positive correlation of leaf orientation value with soil temperatures. Long wave infra-red radiations from the soil probably played a part, even though net radiation did not show significant correlation. There was a level of concord in the results of correlation and regression analyses as soil temperature and average solar radiation were also identified by regression as the variables controlling LOV_{Upper} , while soil temperature alone seemed to control LOV_{Lower} . That would seem plausible because penetration of solar radiation to the lower canopies is often limited by mutual shading thereby leaving long wave infra-red radiation from the soil as the only real radiation source to the lower leaves, hence its effects on LOV_{Lower} . Soil moisture is the primary variable affecting upper and lower leaf angles directly and the effect is negative. This would seem to negate the field observations earlier mentioned, where leaves stood erect on the field upon exposure to an extended period of drought. However, an erect leaf caused by drought stress could either mean a reduced leaf angle or an altered leaf orientation value. Analysis showed that it was more of the latter in this case than the former. At the tertiary level, air temperature strongly influenced air RH negatively and air RH ($P = 0.908$), in turn, exerted a strong positive effect on soil moisture at the secondary level. This means that a humid environment retains more soil moisture but increased air temperature reduces the humidity in the air, indirectly reducing soil moisture in the process. Rainfall had a direct but negligible effect on soil moisture despite its being the only source of moisture to the soil in the environments of this study. It could be inferred, therefore, that while rainfall provides the moisture in the soil, air relative humidity plays a crucial role in its retention. Interestingly, these climatic factors do not exist in isolation; there is constant interactions among them as seen in the relationship of Sm , relative humidity and air temperature described above.

For LOV_{Upper} , total solar radiation exerted strong secondary direct effect on soil temperature and average radiation, the two variables that directly influenced the LOV_{Upper} . The effect of radiation on LOV_{Upper} would make sense considering the different ways in which the sun contributes to different physiological processes in plants via the leaf. As earlier stated – photosynthesis, chlorophyll formation and phototropism are important physiological processes within the leaf that are driven mainly by solar radiation. Soil temperature is the single, most important variable influencing LOV_{Lower} , but like LOV_{Upper} , total solar radiation (tertiary) and average radiation (secondary) interacted to affect soil temperature. As earlier stated, the direct effect of soil temperature on LOV_{Lower} is likely due to the mutual shading by upper leaves blocking solar radiation from penetrating to the lower leaves thereby causing them to respond perhaps to the long wave radiations from the soil. However, total and average solar radiations played big roles behind the scene. Multiple analyses revealed soil moisture was the most important variable controlling LA, while soil temperature was the most important variable that controlled upper and lower LOV. Soil temperature was the only variable contributing directly to LOV_{Lower} and, by far, made the larger contribution to the total R^2 in its interaction with average solar radiation to influence LOV_{Upper} .

A study by Fakorede and Opeke (1985) found air relative humidity and effective rainfall as the climatic variables favouring grain yield at the OAU T&RF. Unfortunately, no canopy architecture indices were assayed in that study. Perhaps leaf angle might have played a dominant role in the results they observed if the leaf parameters had been assayed in the study carried out more than three decades ago. In addition, it is highly probable that the results might have been slightly different if climate change impact had become serious at that time. Prior to that study, Fakorede (1985) had found that planting early in the season in March/April optimized yield at the same location and that yield decreased significantly with delays in planting beyond early April. One could attempt a relationship between those studies and the present study. For instance, LOV_{Upper} has been established in a study by Fayose *et al.* (2022) as the most important leaf architecture index positively influencing grain yield. The same study identified environments planted early in March as some of the best performers for grain yield and LOV_{Upper} . In the same study, leaf angle was also found to influence yield, albeit, indirectly via LOV_{Upper} . That result is not incongruous because of the significant contribution of leaf angle in LOV determination, and the role that air relative humidity plays in the retention of soil moisture (the major factor influencing LA) has been explained above. Perhaps, along with air relative humidity and effective rainfall, leaf angle might have played a significant role in explaining the grain yield performance of the maize varieties evaluated by Fakorede and Opeke (1985), if the study had evaluated canopy architecture characteristics. Grain yield has also been established in the literature as a complex trait controlled by many genes and several environmental factors (Zhang *et al.*, 2020). Thus, no contribution, direct or indirect should be overlooked in our quest to boost yield and ensure food security amidst the prevailing climate change scenarios. The influence of solar radiation variables (average and total) have also been highlighted earlier in this section. A number of studies had found planting maize early with the first few rains in

March/early April maximises yield at the location of this study (Fakorede, 1985; Fayose and Fakorede, 2021b). A study by Fayose (2018) identified total global radiation as the single most important factor favouring higher grain yield at this location. March and April at the location are often the periods with low cloud cover allowing more solar radiation to reach the surface. This might have influenced the result observed in the studies. Maize benefits from a high level of solar radiation and heat.

Physiologically, maize is a C4 plant, and a heat lover. As a result, and as long as temperature does not rise above a threshold, usually 30°C (Abasi *et al.*, 1985), increased solar radiation will increase grain yield. The increased grain yield could be attributed to the efficiency of the upper leaves in converting solar energy into a biological energy, i.e, grain yield. The amount of sunlight trapped within the canopy would have provided more insight on leaf response to solar radiation. Unfortunately, that was not done in this study due to lack of a properly functioning light probe at the period of this study. That result would have provided an explanation to the significant response of LOV to solar radiation observed in the present study. Results also showed that LOV especially of the lower canopy in the hybrid (Oba Super 1) responded to the weather factors in a different manner from other varieties, which in turn, showed different levels of response to the weather factors, an indication that genotype influences maize canopy architecture's response to weather factors. Including many more varieties in the analysis would aid deeper understanding of the genotype x climate interaction effect on maize canopy architecture's response to the environment.

5. CONCLUSION

Upper leaf orientation value, the most important canopy architecture index influencing grain yield, was influenced directly by soil temperature and average radiation, and indirectly by air relative humidity, heat unit, total radiation, and soil heat flux. Lower leaf orientation value was influenced directly by soil temperature and indirectly by average radiation and rainfall. Air relative humidity and rainfall affected leaf angle indirectly via soil moisture, the single most important weather factor directly influencing leaf angle. Environment, especially climate significantly influenced maize canopy architecture in this study. Significant genotypic effect was also observed in maize canopy architecture's response to weather factors.

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