

CANOPY ARCHITECTURE AND GRAIN YIELD OF MAIZE (*ZEA MAYS* L.) IN THE RAINFOREST OF SOUTHWESTERN NIGERIA

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ABSTRACT

Plant architecture is a key factor for optimum productivity in most crops. Unfortunately, this aspect of maize (*Zea mays* L.) crop configuration has received little attention from researchers in the rainforest ecologies of Nigeria. We investigated the effects of the environment on canopy architecture and, in turn, canopy orientation on grain yield 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 canopy architecture, which was quantified with upper and lower leaf angle (LA_{Upper} and LA_{Lower}) and leaf orientation values (LOV_{Upper} and LOV_{Lower}) obtained at the grain-filling stage. At maturity, grain yield, along with some of its components (ear length, ear diameter and kernel row number) were also obtained from all plots. The data were subjected to ANOVA, correlation, regression, and sequential path analyses to determine the relationship of grain yield with canopy architecture. The environment and genotype had significant effects on canopy architecture, grain yield ($P = 0.01$; $R^2 \geq 80\%$), and yield components. Leaf orientation value of the upper canopy (LOV_{Upper}), with correlation coefficient $r = 0.61^{**}$ and direct positive causal effect ($P = 0.61$), rather than LA_{Upper} , LA_{Lower} and LOV_{Lower} , greatly affected grain yield. In conclusion, LOV_{Upper} was the single most important leaf architecture index that positively affected grain yield which, in turn, was influenced greatly by the environment in the rainforest ecology of SW Nigeria.

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

INTRODUCTION

Maize (*Zea mays* L.) is a popular crop in sub-Saharan Africa (SSA) and the popularity has continued to grow because the crop provides a cheap source of calories for the relatively poor population, who process it to different food forms in addition to consuming it boiled or roasted. Unfortunately, factors such as increased urbanization, decreasing soil fertility, poor conditions of climate including climate change are constant and ever growing threats to maize production (Fakorede and Akinyemiju, 2003). Consequently, there is a huge gap between the demand for maize grain and the level of production. Maize production in SSA must increase to meet the constant demand for its grains. Maize has received a lot of attention from agronomists and plant breeders over the years, and much progress has been made in many aspects of genetic improvement, including the development of high yielding, disease resistant, drought tolerant, and nutritionally fortified open-pollinated and hybrid varieties (Badu-Apraku and Fakorede, 2017).

Maize canopy architecture, particularly leaf structure, has received little or no attention from researchers in SSA despite the critical role leaves play in plant nutrition through photosynthesis and other physiological functions. According to Li *et al.* (2015), canopy architecture is a key factor for high productivity in maize because ideal architecture with an erect leaf angle and optimum leaf orientation value (LOV) allows more efficient light capture during photosynthesis, and better wind circulation under dense planting conditions. Erect or erectophile leaves can effectively contribute to maize grain yield by enhancing light capture for photosynthesis, serving as nitrogen reservoirs for grain filling, and enabling denser planting with a higher leaf area index (Vazin *et al.*, 2010). Light has also been implicated for its significant effects on leaf health. Vazin *et al.* (2010) found that leaves closer to the base of the plant exhibited early senescence because of low light penetration to that part of the plant. This supports the finding of Ku *et al.* (2010) that a major limiting factor for high productivity of maize in dense planting is light penetration through the canopy.

Leaf angle (LA), leaf length and width, leaf area index (LAI = leaf area per unit land area) and the LOV are important components of maize canopy architecture. Leaf angle is the measure of the contact between the stem and leaf at the node of attachment. Leaf length is divided into two: the length from the base up to the flagging point, and the length from the base to its arrow-like tip (also called full length). The leaf angle, flagging point and full length are all involved in the determination of LOV. According to Pepper *et al.* (1977), leaf orientation value is a function of leaf angle and leaf length, and is a measure of the leaf area that is properly placed for the optimum interception of light for photosynthesis. The leaf orientation value accounts for the ability of leaves to maintain the same orientation for their entire length. Over the years, an ideotype of maize canopy architecture has been proposed as that with upper leaves more erectophilic in nature and lower leaves more planophilic (Loomis *et al.*, 1969; Mock and Pearce,

1975). This 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 LAI (Mock and Pearce, 1975; Duvick, 2005), and reducing premature leaf senescence.

Improvement of plant architecture has greatly increased maize grain yield during the past few decades (Wang *et al.*, 2011), especially in the developed countries. Optimized plant architecture has rendered most modern maize hybrids more productive due to their tolerance of high plant densities (Huang *et al.*, 2017). Studies by Pepper *et al.* (1977), Ku *et al.* (2010), and Li *et al.* (2015) in the USA and China, have demonstrated that grain yield and other agronomic traits of maize are influenced by canopy architecture. Huang *et al.* (2017) compared two modified leaf arrangements with the original (unmodified) arrangement in maize, and observed significant reduction in plant and ear heights, leaf size, leaf orientation, and grain yield performances in the modified leaf arrangements. There is paucity of information on this subject generally in SSA, but particularly in the tropical rainforest ecologies of Nigeria. It is imperative to determine if there is significant relationship of maize grain yield with canopy architecture in the rainforest ecology of SW Nigeria. Plant breeders could potentially leverage this information to investigate deeper on the genetics of canopy architecture with a view to modifying the crop sufficiently to boost yield.

The primary objective of the present study was to investigate the relationship between maize grain yield and canopy architecture in multiple environments in the tropical rainforest ecologies as typified by Ile-Ife, SW Nigeria.

MATERIALS AND METHODS

1. Experimental location, design and planting material

The study was conducted 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 have been described in an earlier report (Fayose and Fakorede, 2021a). 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 OPVs included White DT STR SYN1-TZL Comp. 1-W, TZL Comp. 4 DT F₂, TZL Comp. 1 C6/DT – SYN – 1 –W, all of which were drought tolerant (DT) and of intermediate/late maturity, and ACR 94TZE Comp 5 C₃ (early maturing). Oba Super 1, an intermediate/late single-cross hybrid obtained from Premier Seeds, Zaria was the fifth variety. The four OPVs were obtained from the IITA Maize Improvement Program. All five varieties are white-grained, high yielding and have been released for commercial production in Nigeria and several other West and Central African (WCA) countries.

The experiments were planted weekly (environment) from March to November each year. However, there were some weeks where planting could not be done due to some logistic problems, but 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; and 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. Prior to planting, the experimental land was ploughed and harrowed and the seeds were treated with Apron* which contains thiamethoxam, mefenoxam (metalaxyl-M) and difenoconazole, to control damage by soil-borne diseases and insect pests. 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. Fertilizer was applied immediately after thinning at the rate of 60 kg ha⁻¹ each for N, P₂O₅ and K₂O. Primextra, which contains atrazine (2-chloro-4- (ethyl amino)-6-isopropylamino-s-triazine) and alachlor (N-(methyl-2-methoxy-ethyl)-2-ethyl-8-methyl-chloroacetanilide) as active ingredients was applied as post-planting, maize pre-emergence herbicide at the rate of 5 lha⁻¹. Further weed control was done using paraquat (N,N'-dimethyl-4,4'-bipyridinium dichloride), carefully applied as a post-emergence, non-selective and contact herbicide at the rate of 3.0 lha⁻¹.

2. Data collection

Data were collected on leaf angle and orientation for the upper and lower leaves. The upper leaf angle and orientation (LA_{Upper} and LOV_{Upper}) were determined using the leaf immediately above the ear, while the lower leaf angle and orientation (LA_{Lower} and LOV_{Lower}) were taken from the leaf immediately below the ear. Leaf angle was measured using a properly calibrated clinometer smartphone application (Pioneer, 2016); while the leaf length up to the flagging point (L_{fp}), and the full length (L_t) were measured using a flexible meter rule. Leaf orientation value, a measure of the portion of the canopy that is properly positioned for the interception of solar radiation, was obtained from the following equation (Pepper et al., 1977):

$$LOV = \sum_{i=1}^n LA * \left(\frac{L_{fp}}{L_t} \right) / n \text{ where } n = \text{no. of plants measured} = 10.$$

Leaf orientation values were also used to categorize the varieties into large (≥ 19), medium (16-18.9) and small (< 16). Mean statistic of LOV_{Upper} and grain yield was calculated for all environments within each group. Furthermore, 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.

3. Statistical analysis

Variance analysis for a mixed model was done on all data using PROC GLMM of Statistical Analysis System (SAS, 2000). Variety was considered a fixed factor while environment and its interaction with variety were considered as random factors. The linear additive model for the ANOVA was: $Y_{ijk} = \mu + \alpha_i + \beta_{j(i)} + \lambda_k + \alpha\lambda_{(ik)} + \varepsilon_{ijk}$, in which Y_{ijk} is the observed measurement of the k^{th} genotype grown in the j^{th} rep under the i^{th} environment; μ is the grand mean; α_i is the main effect of the i^{th} environment, $i=1,2,\dots, 39$ or 42 ; $\beta_{j(i)}$ is the effect of the j^{th} replication nested within the i^{th} environment, $j=1,2,3$; λ_k is the effect of the k^{th} genotype, $k=1,2,\dots,5$; $\alpha\lambda_{(ik)}$ is the first order interaction of the i^{th} environment with the k^{th} genotype, and ε_{ijk} is the random error (residual) term. 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. 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 which, in this case, were leaf architecture indices, were organized into first and second order, based on their contributions to the total variation in the predicted traits (grain yield) with minimized multicollinearity. To perform the stepwise regression analysis, grain yield was regressed on the leaf architecture indices to identify those with significant contributions to grain yield at $P \leq 0.05$, and they were categorized as first order variables. The first-order variables thereafter were each regressed on other leaf architecture traits which were not in the first order category, to identify the leaf architecture traits with significant contributions to grain yield through the first-order variables. These variables were classified as second order variables. 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.

RESULTS

Results from the variance analysis showed highly significant environmental (E) and varietal (V) effects for all leaf architecture indices (Table 1). There were no significant ExV effects except for LA_{Lower} at $P \leq 0.05$. The leaf measurements were quite uniform, with CVs of 13 and 14% for leaf angle and leaf orientation value, respectively and R^2 values of 78% for leaf angle and 79 to 83% for leaf orientation value. As expected, the environment and variety greatly influenced grain yield and yield components (Table 2). Apart from ear diameter (ED), grain yield along with its components were significantly affected by the environment. Indeed, there was maize genotypic response to the environment, as indicated by the statistically significant variety x environment interaction for traits of the adult maize plant except ED and kernel row number (KRN). The fact

that grain yield and ED had fairly high CV values (31% and 36%, respectively) where EL had a relatively lower CV (10%) is surprising, given ED and EL had similar mode of measurement. Both ED and EL, however, had comparable R^2 values (about 75 and 76% for ED and EL, respectively), while yield had a slightly higher R^2 value of about 85%. The KRN had the lowest CV (6%) value, although with the lowest R^2 (60%) value too.

Table 1: Mean squares from the ANOVA of upper and lower leaf angle (LA) and leaf orientation value (LOV) of five maize varieties evaluated at the OAU T&R Farm, Ile-Ife in 2016 and 2017.

Source	Leaf angle			Leaf orientation values (LOV)		
	Df	LA _{Upper} [†]	LA _{Lower}	Df	LOV _{Upper}	LOV _{Lower}
Env	41	100.99***	95.23***	38	72.19***	43.09***
Rep/Env	84	16.91	8.92	78	6.87	5.52
Variety	4	2601.13***	1405.14***	4	1256.52***	780.51***
Env x Var	164	15.89	12.98*	152	6.51	6.49
Error	336	15.47	10.37	312	6.10	5.18
Total	629	37.79	25.26	584	19.18	13.35
CV,%		13.45	13.35		14.11	14.21
R ²		0.78	0.78		0.83	0.79

*, ***- F statistic significant at 0.05 and 0.001 level of probability, respectively.

CV- Coefficient of variation

R²- Coefficient of determination

† - LA_{Upper} = upper leaf angle in degree, LA_{Lower} = lower leaf angle in degree.

Table 2: Mean squares from the ANOVA of grain yield and its components for five maize varieties planted over several environments at the OAU T&R Farm in 2016 and 2017.

Source	DF	Yield (t/ha)	Yield components			
			DF	Ear length [†]	Ear diameter	KRN
Env (E)	41	7.61***	40	23.08***	50.80***	3.26***
Rep/Env	84	0.49***	82	1.98	3.65	0.74
Variety(V)	4	4.76***	4	23.42***	4.31	10.04***
ExV	164	0.45***	160	2.65***	2.40	0.77
Error	336	0.22	328	1.53	2.82	0.64
Total	629	0.83	614	3.43	5.96	0.92
CV, %		30.67		10.08	36.43	6.01
R ²		0.86		0.76	0.75	0.63

*, **, ***- F statistic significant at 5%, 1% and 0.1% level of probability, respectively.

CV- Coefficient of variation

R²- Coefficient of determination

[†] ear length and ear diameter are in cm, KRN = kernel row number.

The rankings of the environments were different for each of the canopy architecture indices, with Env 1 having the largest mean values across indices (Table 3). A quick glance at the grain yield columns would reveal that Env 1 produced a correspondingly high grain yield value. Upper leaf angle was narrowest in Env 47, 17, 12 and 16; and largest in Env 1, 41, 5 and 30. For LA_{Lower}, it was Env 9, 10, 20 and 17 that had the narrowest angles, while Env 1, 41, 3 and 6 had the largest angles. At the larger end of leaf orientation value, Env 1 was prominent, with 2, 6, 19 and 29 also consistent in no definite order for each of LOV_{Upper} and LOV_{Lower}. It is noteworthy that Envs 1, 2 and 29 were among the highest performers for grain yield, an early indication that leaf orientation value might be positively correlated with grain yield. At the narrow end of LOV, Env 45 was narrowest for both upper and lower LOV, other environments that followed for both leaf orientation value indices showed no specific trend. Leaf angle and orientation were narrowest in the hybrid (Var 1) and Var 4; LA was largest in Var 2, LOV_{Upper} in Var 5, and LOV_{Lower} in Var 3 (Table 4). Even though Var 5 had some of the largest values for leaf angle and orientation, with correspondingly high grain yield, Var 4 with similar performance for grain yield had consistently low values for leaf angle and orientation. This suggests that grain yield in different maize varieties might respond differently to the leaf architecture indices.

Table 3: Ranking of the top and bottom ten environments for mean values of angle and orientation of leaves as well as grain yield for five maize varieties evaluated in 42 environments at the OAU T&R Farm in 2016 and 2017.

Rank	LA _{Upper} [†]		LA _{Lower}		LOV _{Upper}		LOV _{Lower}		Grain yield	
	ENV	MEAN	ENV	MEAN	ENV	MEAN	ENV	MEAN	ENV	MEAN
1	47	25.26	9	20.35	45	13.50	45	13.92	1	3.93
2	17	25.36	10	20.35	17	14.72	37	14.32	29	3.22
3	12	25.84	20	20.99	47	15.00	38	14.40	2	3.18
4	16	26.01	17	21.28	16	15.53	47	14.44	32	2.39
5	9	26.56	12	21.73	44	15.66	39	14.54	31	2.26
6	10	26.56	47	21.78	10	15.70	48	14.61	11	2.10
7	11	26.97	15	21.99	9	15.88	17	14.62	18	1.98
8	8	27.28	37	22.08	46	16.13	16	14.69	19	1.97
9	44	27.31	39	22.11	39	16.19	44	14.71	7	1.91
10	48	27.33	18	22.13	14	16.29	9	14.75	44	1.87
33	4	30.95	34	25.49	33	18.34	7	17.02	5	0.96
34	6	31.44	30	26.34	32	18.57	32	17.07	34	0.95
35	2	32.39	2	26.72	20	18.71	35	17.13	39	0.94

36	3	32.42	29	26.84	30	19.03	41	17.38	3	0.90
37	29	32.68	4	27.30	41	19.55	30	17.55	40	0.88
38	19	33.20	5	27.49	6	19.85	19	18.22	38	0.86
39	30	33.21	6	28.21	19	21.40	2	19.07	8	0.84
40	5	33.55	3	28.32	2	22.89	29	19.18	37	0.77
41	41	34.43	41	29.90	29	23.21	6	19.93	4	0.70
42	1	36.63	1	31.29	1	23.23	1	21.37	50	0.42
LSD _{0.05}		2.83		2.31		1.77		1.64		0.33

LSD – Least significant difference

† - 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.

Table 4: Mean and LSD values of leaf angle and orientation and grain yield of five maize varieties monitored over several environments at the OAU T&R Farm in 2016 and 2017 cropping seasons.

LA_{Upper}^{\dagger}		LA_{Lower}		LOV_{Upper}		LOV_{Lower}		Grain yield t/ha	
Variety ϕ	Mean	Variety	Mean	Variety	Mean	Variety	Mean	Variety	Mean
1	22.59 [†]	1	19.47	1	12.16	1	12.00	5	1.74
4	26.50	4	21.68	4	16.55	4	14.82	4	1.67
3	31.81	5	26.02	3	19.51	2	17.68	2	1.55
5	32.02	3	26.62	2	19.60	5	17.75	1	1.33
2	33.31	2	26.80	5	19.75	3	17.85	3	1.31
LSD_{0.05}	0.97		0.80		0.64		0.59		0.115

LSD – Least significant difference

[†] - See Table 3

ϕ - Var 1 = Obasuper 1, Var 2 = White DT STR SYN1.- TZL Comp. 1– W,

Var 3 = ACR 94 TZECComp 5C₃, Var 4 = TZL Comp. 4 DT F₂, Var 5 = TZL Comp. 1 C6/DT – SYN – 1 – W.

Correlation analysis showed that leaf orientation value rather than leaf angle, had profound effects on yield and its components. Upper leaf orientation value (LOV_{Upper}) and LOV_{Lower} had fairly strong positive correlations with grain yield and ear diameter but weaker though statistically significant positive correlation with kernel row number (Table 5). It would seem, however, that ear length responds to LOV_{Lower} only; it had no significant correlation with LOV_{Upper} whereas ear diameter had significant positive correlation with both upper and lower LOV. Leaf angle, on the other hand, had significant correlation with only ear diameter. Therefore, leaf architecture would seemingly influence the girth of the ear rather than the length. Stepwise multiple regression followed by simple linear regression revealed LOV_{Upper} as the important variable influencing maize grain yield with the equation: $\hat{Y} = 0.20X - 1.93$ ($R^2 = 0.38$) and a fairly strong direct causal effect ($P = 0.61$). Other leaf architecture indices had positive indirect effects ($P = 0.805$ and 0.582 for LOV_{Lower} and LA_{Upper} , respectively) and negative indirect effect ($P = -0.443$ for LA_{Lower}) on yield via LOV_{Upper} (Figure 1).

Table 5: Correlation coefficients of leaf angle and orientation with grain yield and its components of five maize varieties planted in 42 environments in 2016 and 2017 seasons at the OAU T&R Farm.

	LOV _{Upper} [†]	LOV _{Lower}	LA _{Upper}	LA _{Lower}	Ear_length	Ear_diameter	KRN	YIELD (t/ha)
LOV _{Upper}	1	0.88**	0.82**	0.71**	0.31	0.52**	0.34*	0.61**
LOV _{Lower}		1	0.76**	0.83**	0.44**	0.59**	0.36*	0.61**
LA _{Upper}			1	0.85**	0.08	0.44**	0.01	0.26
LA _{Lower}				1	0.22	0.46**	-0.02	0.25
Ear Length ^ϕ					1	0.51**	0.70**	0.80**
Ear Diameter						1	0.51**	0.69**
KRN							1	0.68**
YIELD (t/ha)								1

[†] - 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.

^ϕ ear length and ear diameter are in cm, KRN = kernel row number.

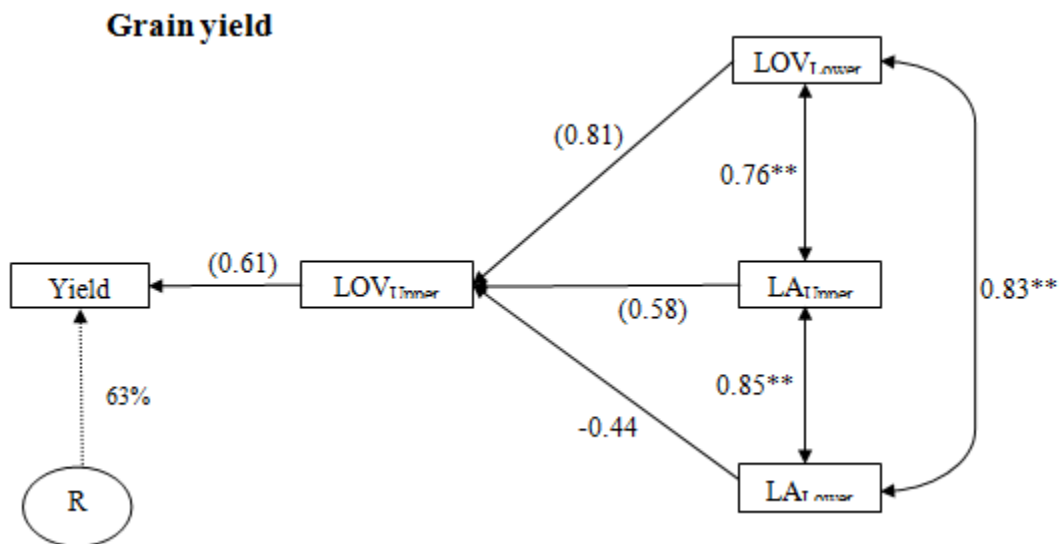


Figure 1: Sequential path-coefficient analysis diagram of leaf architecture indices affecting grain yield. One directional arrows indicate direct effects while double arrows are correlation coefficients. ** Significance at 0.01 level of probability.

The low R² value (38%) observed from the linear regression of grain yield on upper leaf orientation value suggests a somewhat more complex response of grain yield to LOV_{Upper}, that goes beyond a linear relationship. Plotting a quadratic polynomial significantly increased the R²

value to about 55%, increasing the polynomial order to a cubic thereafter resulted in no significant increase in the R^2 value (Figure 2).

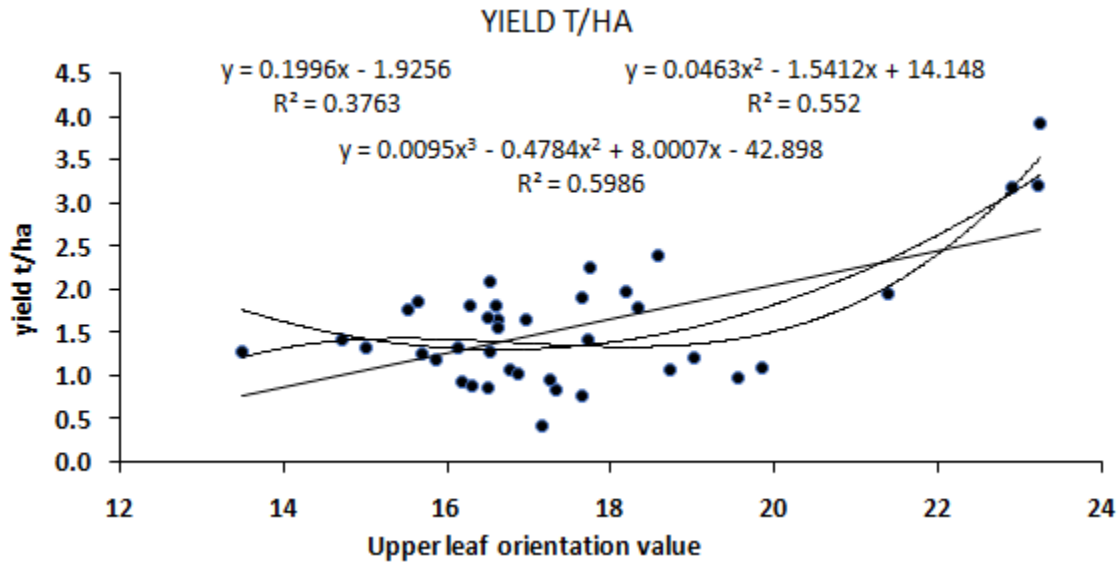


Figure 2: Response of grain yield to upper leaf orientation value for five maize varieties evaluated in 39 environments at the OAU T&RF in 2016 and 2017 cropping seasons.

Table 6 presented the grain yield performance in different planting dates (representing the environments) in a decreasing LOV_{Upper} order. Three different LOV_{Upper} groups (≥ 19 = Large, 16-18.9 = medium and < 16 = small) were generated. Results showed that the large LOV_{Upper} group had significantly higher grain yield than the other two groups which, in turn, were not different from each other (Figure 3). A regression analysis of grain yield on LOV_{Upper} within the group revealed a certainly linear relationship with R^2 value of about 93% (Figure 4), which indicates that the higher the LOV_{Upper} from the group threshold point, the higher the grain yield. Noteworthy also, is the fact that the large LOV_{Upper} group was dominated by the first two environments planted in March each year. Figure 5 further supports the suggestion in earlier results that different varieties seemingly respond differently to LOV_{Upper} . For instance, Var 5 and 4 had the joint highest grain yield despite their contrasting LOV_{Upper} values (19 vs 16, respectively). Similarly, Var 1 and 3 produced comparably low yield despite being on opposite ends in terms of LOV_{Upper} value.

Table 6: Upper leaf orientation value with corresponding grain yield, including three LOV_{Upper} groups and mean grain yield obtained in 39 environments at the OAU T&RF.

S/N	ENVIRON	Planting date	†LOV _{Upper}	YIELD(t/ha)	LOV _{Upper} groups	Mean LOV	Mean yield per group (t/ha)
1	1	16-Mar-2016	23.23	3.93			
2	29	15-Mar-2017	23.21	3.22			
3	2	24-Mar-2016	22.89	3.18			
4	19	07-Sept-2016	21.39	1.97	≥19	21.31	2.23
5	6	20-Apr-2016	19.85	1.09			
6	41	14-Jun-2017	19.55	0.97			
7	30	29-Mar-2017	19.03	1.21			
8	20	15-Sept-2016	18.71	1.08			
9	32	12-Apr-2017	18.57	2.39			
10	33	19-Apr-2017	18.34	1.79			
11	18	31-Aug-2016	18.19	1.98			
12	31	05-Apr-2017	17.75	2.26			
13	49	23-Aug-2017	17.71	1.43			
14	7	27-April-2016	17.66	1.91			
15	37	17-May-2017	17.65	0.77			
16	8	04-May-2016	17.34	0.84			
17	34	26-April-2017	17.27	0.95			
18	50	06-Sept-2017	17.17	0.42			
19	13	15-June-2016	16.98	1.65	16-18.9	17.85	1.44
20	42	15-June-2017	16.87	1.02			
21	35	04-May-2017	16.78	1.07			
22	48	16-Aug-2017	16.63	1.56			
23	12	01-June-2016	16.62	1.66			
24	43	05-July-2017	16.61	1.81			
25	36	10-May-2017	16.54	1.29			
26	11	25-May-2016	16.54	2.09			
27	15	10-Aug-2016	16.49	1.69			
28	38	24-May-2017	16.49	0.86			
29	40	07-June-2017	16.31	0.88			
30	14	03-Aug-2016	16.29	1.81			
31	39	31-May-2017	16.19	0.94			
32	46	02-Aug-2017	16.13	1.32			
33	9	11-May-2016	15.88	1.19			
34	10	18-May-2016	15.69	1.25			
35	44	19-July-2017	15.65	1.87			
36	16	17-Aug-2016	15.54	1.76	<16	16.07	1.42

37	47	09-Aug-2017	15.00	1.34
38	17	24-Aug-2016	14.72	1.43
39	45	26-Jul-2017	13.50	1.29

†Table arranged in descending order of LOV_{Upper} for all variables.

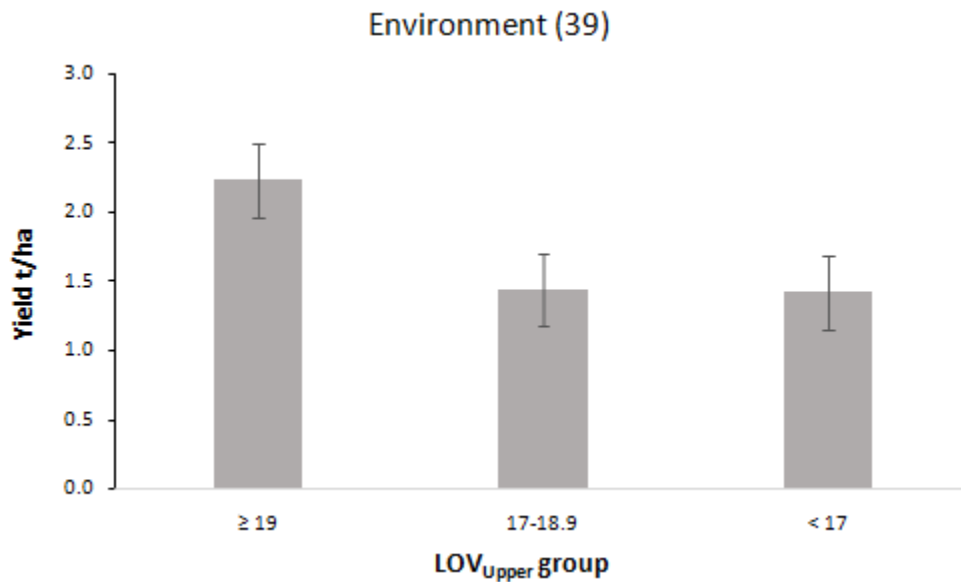


Figure 3: Effect of three groups of upper leaf orientation value on grain yield of five maize varieties evaluated in 39 environments at the OAU T&RF in 2016 and 2017 cropping seasons.

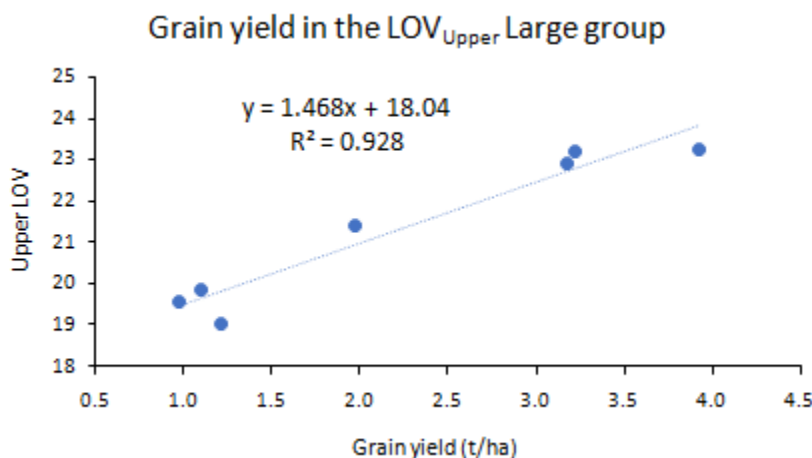
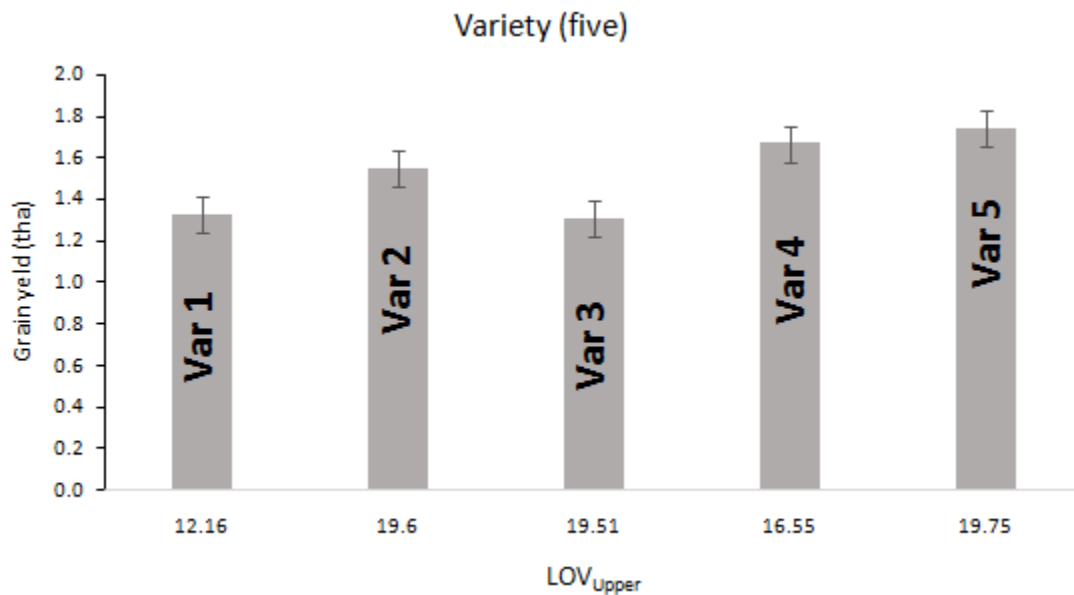


Figure 4: Response of grain yield of five maize varieties to the upper leaf orientation value in the seven environment that makeup the large LOV_{Upper} group.



Var 1 = Obasuper 1, Var 2 = White DT STR SYN1.- TZL Comp. 1- W, Var 3 = ACR 94 TZE Comp 5C₃, Var 4 = TZL Comp. 4 DT F₂, Var 5 = TZL Comp. 1 C6/DT - SYN - 1 - W.

Figure 5: Response of grain yield of five maize varieties to upper leaf orientation value at the OAU T&RF in 2016 and 2017 cropping seasons.

DISCUSSION

The primary objective of this study was to investigate the response of maize grain yield to canopy architecture over several environments. Results of the study revealed a highly significant environmental effect for all canopy architecture indices as well as grain yield along with its components. The largest proportion of the total variation was due to the environment alone. For instance, up to 59 % of the total sum of squares in grain yield was due to environmental effects. The environments in this study were represented by the different planting dates in 2016 and 2017. It is already a well known fact that environmental conditions at a particular location vary widely from day to day, and from one environment to another. Edaphic and, particularly, climatic factors vary widely among environments and account for most of the variations observed as one moves across environments. The environmental factors responsible for the observations in this study are determined in another paper.

The performance of the leaf architecture indices was variable in different environments except for Environment 1 which was consistent for recording the largest means for all leaf architecture indices. Perhaps the most striking results was that most environments with top yields also had large values for LOV_{Upper}. Nutrition in most plants is dependent in no small measure on the leaf. It is, therefore, not surprising that leaf orientation value (LOV) generally influenced maize grain

yield positively. It is surprising, however, that leaf angle (LA) did not influence grain yield in anyway as observed from the results from correlation analysis, given that LA was an important component in LOV determination.

It would seem therefore, that general leaf arrangement particularly length and length to the flagging point influenced maize grain yield to a much greater extent rather than the angle that the leaf makes with the stem per se. That is, the proportion of the leaf flag point to the overall length relative to the angle of the leaf on the stem is of utmost importance. Regression analysis revealed that upper LOV (LOV_{Upper}) was in fact, the most important index influencing yield directly with other variables contributing indirectly to grain yield. This might actually not be surprising. After all, the flag leaf has been implicated to contribute immensely to the assimilates partitioned for maize seed production (Bewley *et al.*, 2013). However, it would be erroneous to assume that the overall maize grain yield is dependent on the flag leaf or other upper leaves for that matter, because of the concepts of photosynthesis, respiration and net photosynthesis or assimilation. If the lower leaves were to be completely shaded, the photosynthate from the upper leaves would be burned in plant respiration and little or no assimilate would be available for seed partitioning and grain filling. Also, the relatively low R^2 value recorded in the simple linear regression of grain yield on LOV_{Upper} indicates that the relationship of LOV_{Upper} and grain yield is not linear. Increasing the order of polynomial proved that the relationship is more quadratic than linear as more variation was accounted for by the regression model when a quadratic curve was plotted. This indicates that yield does not increase significantly or remained flat until an LOV_{Upper} threshold is reached.

Further analysis revealed an LOV_{Upper} threshold value of 19, after which the relationship between grain yield and LOV_{Upper} became linear. That is, yield increased steadily with an increased LOV_{Upper} value once the LOV_{Upper} threshold of 19 was reached. It is safe to assume therefore, that there are other factors controlling grain yield when the threshold LOV_{Upper} value has not been attained, but in situations where the threshold was reached, LOV_{Upper} became a major factor influencing yield. It is already well known that yield is a complex variable, controlled by several genes and a lot of environmental factors. It should be noted that the large LOV_{Upper} group (where the linear LOV_{Upper} and grain yield relationship exist) was dominated by environments planted early with the first few rains in March. Several decades of study at the location, had found planting early with the first few rains in March/early April as the optimum planting window to ensure high yield (Fakorede, 1985; Fayose and Fakorede, 2021b). Investigations are currently ongoing about the factors of the environment that favour the significantly high yield often observed with the early plantings. However, results of this study indicate that canopy architecture might be one of the factors responsible for those results.

Mock and Pearce (1975) had proposed an ideotype of maize in which leaves are preferably erectophile higher up and planophile near the base of the plant. The present study seems at variance with that position; results showed that a more planophile LOV_{Upper} increased grain yield. Solar radiation is more vertical on crops at Ile-Ife (7° N) than at Ames, Iowa, USA (42° N) where Mock and Pearce's study was done. It would seem, therefore, that solar radiation more directly affects the maize crop in the tropics than at angles as in upper latitudes. One could posit that the ideal orientation is the LOV_U that allows maximum light interception by the upper leaves, yet permits adequate penetration to the lower leaves, and LOV_{Lower} that allows the maximum interception of the infiltrating light and minimizes the amount of light reaching the soil surface thereby controlling weed in part, all under the maximum density possible. To achieve this, attention might need to be paid to the plane of arrangement of the upper and lower leaves around the circumference of the stem at each node of attachment, utilizing every angle from 45° to 360° .

Although two of the three varieties with high yield performance (Var 2 and 5) belonged in the large LOV_{Upper} group (with the threshold LOV_{Upper} value of 19), the third variety (Var 4) belonged in the small LOV_{Upper} group. Also, Var 3 that belonged in the large LOV_{Upper} group produced one of the lowest grain yield. Therefore, variety did not seem to influence the response of grain yield in maize to LOV_{Upper} , which was the most important canopy architecture index controlling grain yield in this study. It was the maturity group cum agronomic properties of the varieties that influenced grain yield more. For instance, the three varieties which were of the drought tolerant (DT) and intermediate/late maturity group were consistent for high grain yield, while Var 1 (Oba Super 1) a hybrid, and Var 3 (ACR 94 TZEComp 5C₃) an early variety, both of which did not have the drought tolerant gene/mechanism, produced the lowest grain yield.

CONCLUSION

Conclusively, canopy architecture particularly leaf orientation value significantly influenced maize grain yield in this study; LOV_{Upper} was the single most important leaf architecture index influencing yield. Environment, more than variety, played an important role in maize canopy architecture configuration, and maize yield response to canopy architecture. The LOV_{Upper} was influenced directly by LOV_{Lower} , and both leaf angle indices.

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