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Morphological characterization for leaf architecture in Teosinte (*Zea mays* subssp *parviglumis*) derived BC₁F₂ population of maize

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ABSTRACT: Maize is genetically different from its wild species teosinte (*Zea mays* ssp. *parviglumis*) for various traits since maize has undergone domestication process over 10,000 years ago in the Balsas river valley of Mexico. But some major traits namely plant architecture have seen domestication syndrome which created significant differences between modern maize and its wild progenitor teosinte. It is assumed that some genes/allelic form for plant architecture, particularly for leaf angle, were probably lost during maize domestication and selective breeding. Several reports claim that teosinte have diverse and novel alleles for plant architecture which were absent in modern maize. Plant architecture determines plants canopy, light harvesting capacity and water and nutrient use efficiency. We investigated BC₁F₂ population derived from maize×teosinte cross. The population was subjected to phenotypic evaluation for Leaf Angle (LA), Flag Leaf Length (FLL) and Flag Leaf Width (FLW). Investigation indicates wide variability for LA, FLL and FLW in BC₁F₂ generation. Based on the data and analysis, 305 lines were grouped into different categories based on range of values. Out of 305 BC₁F₂ plants, 216 plants showed >45° leaf angle and 89 plants had <45°, and for flag leaf length and width 305 BC₁F₂ plants showed differential behaviour. The investigation results indicate that teosinte has great significance in broadening and diversification of genetic base of maize germplasm. Further there is enough probability of incorporating erect leaves habit in maize by using teosinte as donor parent that may ultimately help in accommodating more plants per unit area for increasing production and productivity of maize.

Key words: Leaf angle, plant architecture, maize, teosinte

Abbreviations: FLL- Flag Leaf Length; FLW- Flag Leaf Width; LA - Leaf Angle; ML- Maize-teosinte plant, UPA- Upright Plant Architecture

Maize is the most widely cultivated cereal crop after wheat and rice. It was originated in highlands of south-central or southwestern Mexico approximately 10,000 years ago and its immediate progenitor is *Zea mays* ssp. *parviglumis* (Matsuoka *et al.*, 2002). Early maize breeders played a major role in bringing wild species under cultivation through domestication and applied various selection pressures depending on their needs, preferences and environmental conditions grown (Hallauer and Carena., 2009). Plant architecture was one of the important traits of maize which has undergone domestication pressure and virtually modified from grassy species of wild progenitor to highly productive single stem crop species maize. In maize plant architectural traits includes plant height, ear position, number of tillers, leaf angle, leaf size, significantly affects the canopy structure and grain yield. Plant architecture also determines species ability to cope with diseases and

also lodging characteristics (Fei *et al.*, 2022). Canopy structure of crop was determined mainly by leaf area and angle which is responsible for amount of intercepting photosynthetically active radiation, increased planting density, water and nutrient use efficiency intern influences crop yield (Stewart *et al.*, 2003).

Plant architecture has been drastically modified from those of the progenitor teosinte due to domestication and artificial selection exerted by early seed collectors and considered as one of the important domestication syndrome traits (Chen *et al.*, 2021). Modern cultivated maize plant has modified in such way that some traits are showing contrasting phenotypes like leaf angle, number of tillers, numbers of ears per plant, number of rows per cob, leaf length and leaf width (Sahoo *et al.*, 2021). Decreased leaf angle leads to more upright

architecture of plant have certain advantages and helpful in increasing plants density and can increase per hectare yield (Li *et al.*, 2011). Wild progenitor *Zea mays* ssp. *parviglumis* has wide variation and consists of novel alleles for plant architecture which were probably lost in maize while domestication process. Number of genes influencing the growth of leaves and inflorescences were cloned using mutant maize, and significant progress has been made in understanding the genetic principles underlying plant architecture (Liu *et al.*, 2011). Therefore, mining those alleles from wild species and transfer to cultivated species is one of the promising options for breeder for increasing productivity. Tian *et al.* (2019) cloned UPA1 (Upright Plant Architecture1) and UPA2, the two quantitative trait loci conferring upright plant architecture using near isogenic lines developed from *Zea mays* ssp. *parviglumis* and discovered two-base sequence polymorphism in UPA2 which regulates the expression of B3-domain transcription factor ZmRAVL1 which interacts with UPA1 responsible for brassinosteroid production leads to increase of leaf angle. The differential expression ZmRAVL1 in teosinte is due to presence of two-base sequence polymorphism in UPA2 which were absent in cultivated maize. If teosinte allele of UPA2 is combined with the maize allele, a more upright leaf angle may be obtained (Hake and Richardson, 2019). Therefore, based on this information, we hypothesize that teosinte (*Zea mays* ssp. *parviglumis*) can be utilized in breeding programme to derive introgression maize lines with lower leaf angles and other leaf characteristics. Hence, the current study was planned to develop and analyze teosinte (*Zea mays* ssp. *parviglumis*) derived maize lines for leaf angle, flag leaf length and flag leaf width. The investigation was conducted to know phenotypic variation for these leaf traits in teosinte derived BC₁F₂ population.

MATERIALS AND METHODS

Plant materials: The plant materials used in the current study was generated at Norman E. Borlaug Crop Research Centre, Govind Ballabh Pant University of Agriculture and Technology, Pantnagar, India. The teosinte derived BC₁F₂

population utilized for the present investigation was generated by selecting parents having contrasting characters for the leaf architecture characters. The wild progenitor of maize Teosinte (*Zea mays* ssp. *parviglumis*) was used as male parent and elite maize inbred line CML-451 was used as female parent in crossing programme to develop F₁s. The F₁s were backcrossed with maize inbred line and generated BC₁F₁ seeds. The BC₁F₁ seeds were sown and one generation of selfing leads to production of BC₁F₂ Population.

Evaluation for leaf architecture characters

To investigate dynamic changes in leaf characters, the teosinte derived 305 BC₁F₂ Population was evaluated for Leaf Angle (LA), Flag Leaf Length (FLL) and Flag Leaf Width (FLW). The BC₁F₂ Population was sown in 3m row with 60×20 cm planting distance and the data was recorded on individual plants after complete emergence of tassel from flag leaf. The flag leaf length and flag leaf width were measured using standard scale. The leaf angle was measured by taking angle between stem and leaf sheath using standard protractor.

Statistical analysis

The data was recorded on individual plants was subjected to one sample t- test using STAR (Statistical Tool for Agricultural Research) software (Gulles *et al.*, 2014). The scale was developed to categorize the whole population based on their phenotypic values for various traits.

RESULTS AND DISCUSSION

The parental lines taken in the study were possessed contrasting morphological features for leaf characters namely leaf angle, flag leaf length and flag leaf width. The teosinte used as male parent having characters of leaf angle <45°, flag leaf length of 45cm and leaf width of 3.5cm exhibiting narrow leaf characteristics of wild species. The maize inbred line CML-451 used as female parent has characteristics of leaf angle >45°, 30cm of flag leaf length and 4.9cm of flag leaf width representing broad leaf feature of modern cultivated maize. The BC₁F₂ population was analyzed for significant deviations from parental lines using one sample t

test and descriptive statistics on phenotypic variability of data and found wide range of variation for all three parameters leaf angle, flag leaf length and flag leaf width (Table 2).

Leaf Angle: The teosinte derived maize BC_1F_2 population showed significant variation for leaf angle. Angle measured between stem and leaf represents leaf angle. Of the 305 BC_1F_2 plants was measured for leaf angle, 216 plants showed $>45^\circ$ leaf angle and 89 plants had upright leaf angle i.e., $<45^\circ$ (Table 1). Maize yield and canopy photosynthesis was determined by amount of photosynthetically active radiation which was affected by leaf angles and leaf area (Stewart *et al.*, 2003; Liu *et al.*, 2011). Modern hybrids of maize have 14 per cent higher light-interception capacity than maize types introduced between 1930 and 1960 due to development of more erect maize leaves and a higher leaf area index (LAI) (Lee and Tollenaar, 2007). Teosinte has narrow angle compared to maize line which can be transmitted to cultivated germplasm lines to develop upright plant architecture plants better suited to higher density planting and higher yield per hectare basis (Hake *et al.*, 2019). Tian *et al.* (2019) noted a non-coding 240bp region which is responsible for narrow leaf angle in teosinte having two base pair polymorphism which is only present in teosinte and totally lost in maize probably during domestication of species and selective breeding. Similar reports are available for leaf angle in maize and several QTLs were identified by different research groups. Ku *et al.* (2012) identified QTLs for leaf angle, leaf orientation value, leaf length, and leaf width using mapping population of 256 F_2 families evaluated in three different environments and eleven matching mQTLs and fifteen important candidate genes affecting leaf architectural features were found. Likewise, Kumar *et al.* (2019) analyzed teosinte derived BC_1F_4 lines for leaf angle and found significant variation for the trait with reduced leaf angle in derived lines. Similarly, Adhikari *et al.* (2021) investigated teosinte derived BC_1F_3 and BC_1F_4 populations for leaf angle and found that out 126 lines, 34 lines showed reduced leaf angles compared to maize line. We also observed reduced leaf angle in teosinte derived lines probably because of the introgression of genomic regions from

the teosinte.

Flag Leaf Length (FLL) and Flag Leaf Width (FLW): Data were recorded on BC_1F_2 individual plants; hence the one sample t test was used to examine individual plants data without replication. The analysis indicates significant differences ($p=0.001$) across genotypes for flag leaf length and flag leaf width (Table: 2). The 305 plants were classified into three groups based on their length as mentioned in the Table 1. The flag leaf length and flag leaf width have shown wide variation ranging from 12cm to 48.9cm for ML60 and ML15 plants, respectively for flag leaf length and flag leaf width has values ranging from 1.9cm to 7.5cm for ML60 and ML111 plants, respectively. Out of 305 individual plants, 49 plants have shown flag leaf length of small (<20 cm) category, 223 plants exhibited medium flag leaf length (20-35cm) and 35 plants have recorded long flag leaf length (>35 cm). In case of flag leaf width whole population is categorized into three groups i.e., Narrow (<3 cm), medium (3-5 cm) and Broad (>5 cm) having 26, 186 and 23 plants for each of the category, respectively (Table 1). Prominent diversification of flag leaf length and flag leaf width in BC_1F_2 population probably indicates introgression of genomic regions from teosinte into CML-451 background. Such variations provide opportunity to select prominent variants for developing varieties having desirable characteristics for plant architecture. Singh *et al.* (2017) developed teosinte derived BC_1F_3 lines using three inbred lines and evaluated for different morphological features. Flag leaf length and flag leaf width, apart from other traits, showed significant variation and further opined that teosinte can be used

Table 1: Grouping of teosinte derived BC_1F_2 population using leaf architecture traits

Traits	Range of scale		
Flag leaf length	Small (<20 cm)	Medium (20-35 cm)	Long (>35 cm)
Derived plants	49	223	33
Flag leaf width	Narrow (<3 cm)	Medium (3-5 cm)	Broad (>5 cm)
Derived plants	26	186	93
Leaf angle	Broad angle (>45)	Narrow angle (<45)	-
Derived plants	216	89	-

Table 2: Leaf architecture traits of CML 451, Teosinte and Teosinte derived BC₁F₂ population

GENOTYPES	LA	FLL (Cm)	FLW(Cm)	GENOTYPES	LA	FLL (Cm)	FLW(Cm)	GENOTYPES	LA	FLL (Cm)	FLW(Cm)
CML-451	>45	30	4.9	ML34	<45	36	5.3	ML69	>45	30	6
TEOSINTE	<45	45	2.8	ML35	>45	23	2.3	ML70	>45	33	5.6
ML1	<45	33	6.4	ML36	<45	27	5	ML71	<45	26	5
ML2	<45	26.5	3.4	ML37	>45	20.2	4.2	ML72	<45	24	4.5
ML3	>45	32	5.5	ML38	>45	22	4	ML73	<45	27	6.3
ML4	>45	37.2	5.9	ML39	>45	26.2	4.5	ML74	>45	35	5
ML5	>45	36	3.9	ML40	>45	23.5	5.4	ML75	>45	13	2.9
ML6	>45	23	4.5	ML41	<45	24.5	4.7	ML76	>45	30	4
ML7	<45	33.5	5.8	ML42	>45	26	5.3	ML77	>45	30	5
ML8	>45	16.8	3.7	ML43	<45	20	3.5	ML78	>45	33	5
ML9	<45	25.3	4.7	ML44	>45	25.7	5	ML79	<45	28	5.5
ML10	>45	29.5	6.3	ML45	<45	21.1	4	ML80	>45	20	3.7
ML11	>45	26.9	5.1	ML46	>45	23.5	4.5	ML81	>45	22	4.2
ML12	>45	28.9	5	ML47	>45	38.5	6	ML82	<45	23	5.3
ML13	<45	22.6	3.5	ML48	<45	23.4	5.1	ML83	>45	24	3
ML14	>45	28.9	5.2	ML49	<45	33	5.5	ML84	>45	31	6
ML15	>45	48.9	7	ML50	>45	40	6.5	ML85	>45	27.7	5.7
ML16	<45	27.5	5	ML51	>45	20	3.5	ML86	>45	40	7
ML17	>45	20	4.3	ML52	>45	24.5	3	ML87	>45	29	6.3
ML18	>45	22	3.5	ML53	>45	37	5	ML88	>45	34	5.5
ML19	<45	20	5.4	ML54	>45	20	5	ML89	>45	28	5.1
ML20	>45	26	4.2	ML55	>45	20.5	4.5	ML90	<45	24	5.6
ML21	>45	23.4	3	ML56	>45	40	6.9	ML91	<45	28.5	4.8
ML22	<45	22.3	4	ML57	>45	23.5	4	ML92	>45	22.4	4
ML23	>45	22.4	4.6	ML58	<45	35	6.5	ML93	<45	24.7	3.5
ML24	<45	16.5	2.2	ML59	<45	33	5	ML94	>45	26	4.3
ML25	>45	35	4.6	ML60	>45	12	1.9	ML95	>45	31.1	6
ML26	<45	22.4	2.4	ML61	>45	25.5	3.2	ML96	>45	24	3
ML27	>45	19.9	3.3	ML62	>45	25.3	3.2	ML97	>45	39	5
ML28	>45	24	3.1	ML63	>45	22	3.6	ML98	>45	25.5	3.2
ML29	>45	21.4	3.4	ML64	<45	27	4	ML99	>45	23.5	3.8
ML30	<45	24.5	3.5	ML65	>45	20	3.5	ML100	>45	24	4.2
ML31	>45	33	4.3	ML66	>45	26	5.7	ML101	<45	28	6
ML32	<45	24.5	2.9	ML67	>45	17.2	3.5	ML102	>45	27	5.3
ML33	>45	22.8	4.1	ML68	>45	20	4.5	ML103	>45	33	5.4
GENOTYPES	LA ⁽⁰⁾	FLL (Cm)	FLW(Cm)	GENOTYPES	LA ⁽⁰⁾	FLL (Cm)	FLW(Cm)	GENOTYPES	LA ⁽⁰⁾	FLL (Cm)	FLW(Cm)
ML104	>45	44	5	ML139	>45	32.4	5.9	ML174	>45	28	4.6
ML105	<45	37.5	3.5	ML140	>45	18.3	3.3	ML175	>45	20	4.2
ML106	>45	21	2.7	ML141	<45	30	5.2	ML176	>45	27	5.7
ML107	<45	30	5.5	ML142	<45	32	3.7	ML177	>45	24	4

ML108	<45	27.3	4.8	ML143	<45	27.5	3.2	ML178	>45	25.3	4.6
ML109	>45	38.8	5	ML144	>45	24.3	3	ML179	<45	32.1	5.7
ML110	>45	27	3.8	ML145	<45	23.5	3.2	ML180	>45	30.7	4.3
ML111	>45	45	7.5	ML146	<45	21.5	4.2	ML181	>45	34.5	5.5
ML112	<45	33.5	4.8	ML147	>45	20.3	4	ML182	>45	30.5	5.8
ML113	>45	29	4.7	ML148	>45	32.8	3.9	ML183	<45	26	2.8
ML114	>45	25.6	5.4	ML149	>45	23.6	5	ML184	<45	22	2.1
ML115	>45	37	5.2	ML150	>45	26.4	4.8	ML185	<45	29.3	4.4
ML116	>45	35.4	6	ML151	<45	21	4.4	ML186	>45	27.3	3.4
ML117	<45	28.6	4.2	ML152	>45	18.5	3.3	ML187	>45	29	3.4
ML118	<45	28.4	3.7	ML153	>45	24	4.5	ML188	<45	29.3	5.3
ML119	>45	21.5	4	ML154	>45	21.2	4.5	ML189	<45	26.4	6.2
ML120	<45	25.4	3.3	ML155	>45	26	4.7	ML190	>45	29.8	5.3
ML121	>45	21.3	2.7	ML156	>45	21.5	2.4	ML191	>45	14.5	3.4
ML122	<45	34.5	5.3	ML157	>45	24	2.9	ML192	>45	19	3
ML123	>45	22.3	4	ML158	<45	23.2	4.2	ML193	>45	31.2	6
ML124	<45	29.3	5	ML159	<45	22	4.8	ML194	>45	31.4	3.6
ML125	>45	25.7	4.2	ML160	>45	26.8	3.8	ML195	>45	29.6	3.9
ML126	>45	27.8	4	ML161	>45	23.3	3.8	ML196	>45	28.5	6
ML127	>45	24.3	4.9	ML162	>45	33.9	3.9	ML197	>45	22	4.8
ML128	<45	22.8	4.5	ML163	>45	27.6	5	ML198	>45	28.5	5.8
ML129	>45	22.9	3.9	ML164	<45	36	4.5	ML199	<45	32.4	3
ML130	<45	33	4.5	ML165	>45	28	3.5	ML200	>45	17	3.5
ML131	<45	26.8	4.7	ML166	>45	29	3.3	ML201	>45	17.3	4.4
ML132	>45	35.7	5.2	ML167	>45	22	2.4	ML202	<45	27.6	4.6
ML133	<45	38	5.3	ML168	>45	27	6	ML203	>45	17	2.8
ML134	>45	33.4	7	ML169	>45	20.9	2.6	ML204	>45	23.8	4.5
ML135	>45	25	3.6	ML170	>45	42.2	5.8	ML205	>45	41.4	6.5
ML136	>45	37.5	7	ML171	<45	36.6	6.4	ML206	>45	24.3	2.5
ML137	<45	38.3	5.4	ML172	>45	22.2	4.4	ML207	>45	27	3.8
ML138	>45	24	4.4	ML173	<45	41.5	6.2	ML208	>45	23.6	5.3
GENOTYPES	LA⁽⁰⁾	FLL (Cm)	FLW(Cm)	GENOTYPES	LA⁽⁰⁾	FLL (Cm)	FLW(Cm)	GENOTYPES	LA⁽⁰⁾	FLL (Cm)	FLW(Cm)
ML209	>45	26	4.5	ML244	>45	33	4	ML279	>45	25	5.5
ML210	<45	24.8	3.6	ML245	<45	38.5	5.8	ML280	>45	21.3	3.8
ML211	>45	40.5	6	ML246	>45	33.5	6	ML281	>45	23	3.8
ML212	>45	28.4	5.2	ML247	>45	12	3.2	ML282	>45	25	3.7
ML213	>45	15.5	3.4	ML248	>45	39	5.5	ML283	>45	15.3	4
ML214	>45	25.4	4	ML249	<45	31.5	3.5	ML284	>45	18.5	3
ML215	>45	24.1	3.6	ML250	>45	22	5	ML285	>45	14.4	3
ML216	>45	27.2	5.8	ML251	>45	24	5	ML286	<45	30	5
ML217	>45	17.5	2.8	ML252	<45	31	7.5	ML287	>45	17	3.6
ML218	<45	30.5	5.9	ML253	>45	14.7	3.3	ML288	>45	20.6	3.1

ML219	>45	32.5	4.9	ML254	>45	28.2	6	ML289	<45	37	6.8
ML220	>45	44	7	ML255	<45	17.7	4.5	ML290	<45	24	3
ML221	>45	24.2	4.5	ML256	>45	24.4	5.9	ML291	<45	27	5.8
ML222	>45	29.5	5	ML257	>45	26.3	4.5	ML292	>45	16	2.3
ML223	>45	29.4	4.3	ML258	>45	26	5.3	ML293	>45	25	4
ML224	<45	33	6	ML259	<45	19.5	4.4	ML294	>45	25	2.7
ML225	>45	29	6	ML260	>45	22.5	3.7	ML295	>45	16	4
ML226	<45	20	4.4	ML261	>45	37.5	3.6	ML296	>45	20	3.7
ML227	>45	18	4	ML262	>45	33.5	4.5	ML297	<45	19	3.9
ML228	>45	21	4.3	ML263	>45	26.5	5.5	ML298	<45	20	2.6
ML229	>45	30	5.5	ML264	<45	13.5	2	ML299	>45	23	5
ML230	>45	34	6	ML265	<45	30.3	5.8	ML300	>45	13	3.1
ML231	<45	26	4.4	ML266	>45	22.8	4	ML301	>45	23	3.4
ML232	>45	32.5	4	ML267	>45	15.7	2.5	ML302	>45	23	3.5
ML233	>45	19.5	3.3	ML268	>45	31.5	6.5	ML303	<45	22	2.2
ML234	>45	18	2.2	ML269	>45	27	4	ML304	<45	18.4	3.4
ML235	<45	14	2.6	ML270	>45	21	4.3	ML305	>45	23.9	4.3
ML236	>45	15	3.5	ML271	>45	37.5	6	Mean	-	26.59	4.46
ML237	<45	23	4.4	ML272	>45	25	4.4	StdDev	-	6.68	1.15
ML238	>45	27.5	4.9	ML273	<45	33.2	4.4	SE_Mean	-	0.3810	0.0656
ML239	>45	28	5.3	ML274	>45	13	3.8	+ Variance	-	60.78	68.01
ML240	>45	19.5	2.6	ML275	>45	27	5.2				
ML241	>45	28.5	5.7	ML276	>45	22	4				
ML242	>45	30	3.5	ML277	<45	33.5	5.6				
ML243	<45	20	5.5	ML278	>45	20	2.5				

successfully for diversification and enhancement of maize germplasm. Similarly, Adhikari *et al.* (2020) reported modification in flag leaf length and flag leaf width in individuals of the BC₁F₅ population. Whenever wild species genomic introgression observed, considerable changes in gene expression are expected probably due to cis regulation of some genes while trans or both cis and trans regulation of other genes of both wild and cultivated species leading to wide range of variation (Alonge *et al.*, 2020; Haas *et al.*, 2020). Lemmon *et al.* (2014) assayed F₁ hybrids and parental lines for three different tissue types to examine the genome-wide cis and trans regulatory differences between maize and teosinte using RNA sequencing and found that domestication encouraged up-regulation of gene expression because genes with cis differences frequently showed greater expression of the maize allele than the teosinte allele and 17,000 genes are documented which are undergone cis and trans regulation alterations between maize and teosinte. Ku *et al.* (2012) has done QTL mapping for leaf length and leaf width and identified five QTLs for each of the traits located on chromosomes 3, 5, and 7 and chromosomes 1, 2, 7, and 8 explaining phenotypic variation 53.16% and 34.13%, respectively.

CONCLUSION

In the present study, introgression plant architecture (Flag leaf length, Flag leaf width and leaf angle) traits from wild progenitor *Zea mays ssp. parviglumis* were studied. Consequently, 305 teosinte derived BC₁F₂ lines were developed and investigated for phenotypic variation for leaf angle, flag leaf length and flag leaf width traits. Population exhibited wide range of variation for the traits which provide an opportunity for the breeder to think about prebreeding strategies on priority basis to exploit some of the traits which have experienced a

“domestication bottleneck” which are lost in domestication process. Especially in case of leaf angle, the novel alleles for reduced leaf angle lost in maize during the domestication and evolution can be transferred and exploited to increase yield of crop plants. Our results clearly indicates that teosinte can be effectively utilized in breeding programme to derive introgression lines with narrow leaf angle along with optimum flag leaf length and flag leaf width. Apart from these traits, *parviglumis*-teosinte also possessed many desirable allelic variants that may also be prospected while planning for pre-breeding programme for diversification of maize germplasm.

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