

Print ISSN : 0972-8813
e-ISSN : 2582-2780

[Vol. 19(1), January-April, 2021]

Pantnagar Journal of Research

(Formerly International Journal of Basic and
Applied Agricultural Research ISSN : 2349-8765)



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Selection of teosinte (*Zea mays* subsp. *parviglumis*) predomestication alleles to inflate maize genetic resources

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ABSTRACT: Domesticated maize is the consequence of diminished variability and genetic erosion, while wild teosinte is the opulent source of genetic variation in some of the desirable agronomic and kernel traits which are meant to be exploited in maize more through the wide hybridisation to boost up its germplasm amelioration. Very unlikely numbers of researches have been carried on improvement of predomestication alleles. To exploit the variation for some of the novel traits, the teosinte introgressed maize F₁ hybrids were analysed for the variability parameters, existing variance and association analysis in this paper. Traits namely number of tillers and main stalk, number of brace roots, plant height, kernel weight, FFD, and kernel area showed high variability which can be used further in useful selection for maize improvement. Simple correlation analysis was analysed for the traits which shows significant positive association of 1000-kernel weight with the other kernel traits. The experiment thus emphasizes the identification and improvement of more desirable predomestication alleles towards the direction of diversity in maize germplasm.

Key words: Correlation, maize, predomestication alleles, teosinte, variability

Maize, the queen of cereals is a result of rapid evolution and selective breeding from its wild progenitor and it has phenotypically transformed itself according to the human selection with adaptation to different environmental conditions. The archaeological findings show the domestication of maize to be occurred between 10,000 and 6250 years ago in south Mexico (Piperno and Flannery, 2001). Artificial selection in only 2-4% genes (the critical factors which can be known as “predomestication alleles”) of maize became the cause of “domestication bottleneck” as a reason of which maize lost genetic diversity as compared to teosinte from which it was domesticated (Wright *et al.*, 2005). Absence of inter-allelic diversity in the inbred × inbred biparental population restricts the detection of variation in the genes. So, breeders have to develop the teosinte-introgression population for evaluation complementary teosinte allelic diversity in maize. In our breeding programme, among the teosintes, the most compatible immediate progenitor teosinte (*Zea mays* subsp. *parviglumis*) was used for enhancement of maize germplasm by making crosses between teosinte and maize to develop teosinte derived lines. Adhikari *et al.* (2019) analyzed maize and teosinte using 91 SSR markers and observed approximately 25% similarity among the two indicating larger variations between the two.

Flowering time in maize is a polygenic trait having high environmental effect. Maize is monoecious specifically protandry in nature while teosinte-*parviglumis* exhibits protogynous behaviour. At flowering stage, water deficiency may cause delayed silking that results in large

anthesis silking interval (ASI) and failure of fertilization (Westgate and Bassetti, 1990). However, the protogynous behaviour of teosinte can be a blessing to deal the moisture stress. In case of plant morphology, in teosinte the upper lateral branches arising from juvenile and adult nodes are elongated with a tassel in tip (Doebley *et al.*, 1997) whereas, maize has shortened the lateral branches and tipped by ears. The shortening of lateral branches in maize led to more enclosure of ears with husk leaves. While teosinte carries more number of basal tillers, maize carries little branching at lower nodes with an occasional tiller in exception. More number of tillers is one of the survival strategies of teosinte; however, it has lower yield potential. Modern maize has a single thick, fibrous stalk improves the ears, plant density and yield as well (Studer *et al.*, 2011). Hence the trait must be in consideration for maize enhanced prolificacy by utilizing teosinte as a potent donor. As domestication acts, plant height of maize inbreds becomes shorter than the wild. However, in general tall and leafy cultivars require low densities to maximize grain yield per area (Aldrich *et al.*, 1986). In forage crops improvements in characters such as plant height, number of leaves/plant, and stem diameter can help improve fodder yield. The artificial selection in maize was diverted more towards the seed yield sacrificing shoot tillering. This declination was the result of increased expression of the major gene *Teosinte Branched 1 (Tb1)* in shoot primordial so the plants compensated the changes in crown, brace and lateral root growth and architecture (Gaudin *et al.*, 2011). Brace roots are generated from first 2-3 above ground nodes (Hoppe *et al.*, 1986). Brace roots are present in large number in teosinte plants and provide a strong anchorage, lodging resistance, nutrient supply

mainly nitrogen uptake and oxygen supply in water logging condition. These roots are reported to be associated with nitrogen fixation properties of some in Sierra land race from Brazil (Deynze *et al.*, 2018). However, the maize inbreds show less number of aerial roots.

During domestication the seed size is increased as compared to progenitors in almost all the crops including maize. The teosinte ear carries sealed kernels with stony casing which is only about 5 to 12 in number. Whereas, maize ear can bear 500 or more kernels and the kernels are naked without any fruit case covered by papery husk leaves. Kernel traits, kernel number is dependent on kernel row number and ear length whereas the other trait kernel weight depends on kernel size, shape (roundness and length/width ratio), and composition. Seed size is a valuable trait in most of crop plants (Moles *et al.*, 2005) in which larger seeds carry so many benefits such as more nutritious, easier to harvest, smooth processing and the small seeds are mostly related to the weediness (Susko and Doust, 2000). Corn seed size and shape depend on genetics, location and the structure of kernels on the ear (Chaudhry and Ulah, 2001) that even one ear can have kernels of different size and shape as the position of seed on the ear affects both seed size and shape (Ilbi *et al.*, 2009). Grain yield performance of large seeds is higher than small seeds (Graven and Carter, 1990). Seed size had significant effect on ear diameter, ear length, number of kernels per ear, ear weight, 1000-kernel weight, hectolitre weight and grain yield of corn (Kara, 2011).

Presently, the variability in the maize crop has been reached to plateau mainly because of demography and selection bottlenecks (Tenaillon *et al.*, 2004). The exploitation of variability present in the teosinte by analysing various parameters along with efficient selection for strongly associated beneficiary traits by evaluating the teosinte derived lines from different crosses can be the major aim to achieve for a breeder. The introgression lines in literature, indicate grain yield per plot, ears per plant, reduced ASI, protogyny behaviour are among the traits that showed more introgression effect of teosinte alleles (Singh *et al.*, 2017; Adhikari *et al.*, 2019). Hence, an insight into the magnitude of variability present in a teosinte introgressed maize population is needed in order to enhance maize germplasm and to ensure availability of diverse alleles for yield, quality and stress tolerance in future to sustain the maize improvement programme.

MATERIALS AND METHODS

The present investigation was conducted at N. E. Borlaug Crop Research Centre, G. B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand for

field evaluation. Three inbred lines of maize viz., CAL-1444, CAL-159 and CML-451 were crossed with wild teosinte (*Zea mays* subsp. *parviglumis*) in 2018 *kharif*. The resultant F₁s were designated as CI for CAL 1444 × Teosinte, CII for CAL159 × Teosinte and CIII for CML451 × Teosinte for further use in the paper. The F₁s were grown in *kharif* 2019 in four row plots of 4.0 meter spaced to each other at 75 cm with a non-replicated trial. Agro-morphological trait data were recorded for 10 plants each from the parental lines and F₁ plants for days to anthesis (DA), days to silking (DS), plant height (cm), number of tillers and main stalk and number of brace roots and represented in Figure 1. After harvesting, size and shape traits of kernels i.e., 1000-kernel weight (KWT) (g), kernel width (KW) (cm), kernel length (KL) (cm), kernel area (cm²), perimeter (cm), length-width ratio (l/w), roundness and factor form density (FFD) (g/cm³) were analysed by the software ImageJ (32 bit) by taking 20 random samples of seeds each for P, P₁ and F₁ generation (Figure 2). The mean values, range, standard deviation, variance, coefficient of variance, skewness and kurtosis of the parents and F₁s for these traits were analysed and represented in Table 1 and 2. The ratio of length and width (l/w) and the factor form density (FFD) were calculated from the raw data. A factor, referred to as “Factor Form-density” (FFD) describes the differences in grain structure (density) and the deviation from a cylindrical form. This expresses the variation in grain weight not accounted for by differences in grain length and width (Giura and Saulescu, 1996).

Factor Form Density = Grain weight/grain length × width.

Skewness, kurtosis and simple correlation analysis was done using IBM-SPSS Statistics Version 20 and the association between different traits and 1000-kernel weight was analysed.

RESULTS AND DISCUSSION

Coefficient of Variation

Coefficient of variation (CV) is often used to measure and compare variation of quantitative traits (Pelabon *et al.*, 2020). It is a mean- standardized measure of variation indicating the scope of exploiting relative variability for further improvement of the various traits. High CV (>20%) is often related to experimental variability, so for more accuracy, observations from replicated trials or multi-location trials are more reliable. Selection based on these characters would facilitate successful isolation of desirable genotypes because response to selection is directly proportional to the variability present in the material.

Skewness and Kurtosis

The interpretation will be for a particular trait. The

positive skewness indicates the presence of complementary epistatic gene action that implies the slow gain with mild selection and faster gain with intensive selection while with negatively skewed distribution indicates duplicate gene interaction and shows rapid genetic gain under mild selection from the existing variability (Roy, 2000). The positive values of kurtosis (>3) indicate leptokurtic curve (under control of relatively few segregating genes and narrow variability), while kurtosis less than three, indicates platykurtic curve (controlled by many genes and wider variability) and if values are zero, it indicates mesokurtic *i.e.* normal distribution. The character with platykurtic nature is more diverse and more eligible for selection.

Days to anthesis and days to silking

General observation shows the trait DA and DS varies with date of sowing and season. Day length is an important determining factor in the time of floral initiation in plants was first reported by Garner and Allard (1920). In this experiment inbred lines CAL-1444, CAL-159 and CML-451 showed the general protandrous nature as days to anthesis ranged from 55-60 days and days to silk emergence ranged from 57-63 days; however, protogynous behaviour was observed in teosinte as silk emergence took place in 88 days, two days before anthesis started (90 days). Similar findings of early flowering behaviour of maize were found in literature describing the dominance of maize over teosinte for short day flowering (Langham, 1940), high expression of *ZmCCT* alleles in teosinte (Hung *et al.*, 2012). Protogynous teosinte was also observed in the studies of Magoja and Pischedda (1994) in *Z. diploperennis*. The F_s of these maize lines with teosinte showed earlier flowering than both the parents used in the crossing and also earlier than the

population mean (59.85 days). The results were in agreement with Liang *et al.*, (2018) describing the over expression of *ZmMADS69* allele in the maize resulting early flowering in maize-teosinte hybrids. The hybrids of cross CI and CIII had days to anthesis of 54 and 52 days and days to silk emergence of 56 and 55 days, respectively. In F_s of CII, a day to silking (47 days) was earlier than days to anthesis (50 days) showing protogynous flowering behaviour. The results were akin to Singh *et al.* (2017) and Adhikari *et al.* (2019) who found protogyny in teosinte derived maize population. The obtained protogynous lines in teosinte introgressed maize population can lead the research towards the exploitation of diversity in flowering habit of teosinte. High CV ($>20\%$) in both the traits may indicate presence of high variability for the trait because of the teosinte allele introgression.

Number of tillers and main stalk

Teosinte possesses tillering habit and in the investigation multiple basal tillers (5.5) were observed. In case of all the three inbred lines, only single main stalk was noted. This reduction in tillering habit of maize was explained by Dong *et al.* (2017) that, during domestication process the tiller suppressor genes *grassy tillers1 (gt1)* and *tassels replace upper ears1 (tru1)* were targeted by *teosinte branched1* gene (*tb1*) by various protein products, hence the single stalk in maize arose by suppressing the outgrowth of tiller buds. However, the F_s hybrids showed tillering behaviour where number of tillers varied from 2.4 in CIII to 4.6 in CII. Similar findings were mentioned by Rogers (1950) reporting multiple tillering in F_s, suggesting that F_s were inclined more towards the teosinte parents indicating some degree of dominance for the tillering habit of the teosinte parent. Pásztor and

Table 1: Estimates of different parameters in parents and F₁ plants for agro-morphological traits

Sl. No.	Lines	DA	DS	Number of tillers and main stalk	Plant height (cm)	Number of brace roots
PARENTS						
1	Teosinte	90	88	5.5	270.6	21.2
2	CAL 1444	60	63	1	81.4	16
3	CAL 159	55	57	1	122	11
4	CML 451	58	60	1	104	4.2
F₁ HYBRIDS						
5	CI	54	56	3	170.8	47.2
6	CII	50	47	4.6	162.4	30.6
7	CIII	52	55	2.4	185.6	19.4
	Range	50-90	47-88	1-5.5	81.4-270.6	4.2-47.2
	Mean	59.85	60.85	2.64	156.68	21.37
	Std. Deviation	13.71	12.95	1.84	62.83	14.06
	Variance	188.14	167.81	3.38	3948.52	197.91
	C.V. (%)	22.91	21.28	69.56	40.10	65.82
	Std. Error of Mean	5.18	4.89	0.69	23.75	5.31
	Skewness	2.31	1.82	.65	.83	.97
	Kurtosis	5.68	4.23	-1.18	.89	1.17

DA- Days to anthesis, DS- Days to silking

Borsos (1990) reported profuse tillering in maize $\times$ teosinte (*Z. mays* subsp. *mexicana*) F_s and F_s with teosinte characteristics having more number of tillers, high green matter production and better nutritional quality with respect to lysine, aspartic acid and other amino acids. While working on backcross derived lines of maize $\times$ teosinte cross, Singh *et al.* (2017) and Adhikari *et al.* (2019) noted sizable number of lines with proliferacy. In present investigation, very high CV value (69.56%) for trait showed a huge variation is present for the trait in the populations.

Plant height

Teosinte is a tall plant having height about 270.6 cm, however height of teosinte may vary depending season and time of sowing. The three inbred lines had plant height shorter than the teosinte. The F₁ hybrids showed intermediate heights between both the parents. F₁ plants of CIII are of the highest height (185.6 cm) among the F_s whereas the CII had the shortest (162.4 cm). Similar findings were reported by Teng *et al.* (2013) describing the reason for this increase in height may be due to the more contribution of teosinte towards the trait or otherwise the high level expression of a gibberellins (GA) 3-oxidase by gene *ZmGA3ox2*. Wang *et al.* (2008) also had similar findings in the advanced backcross generations of maize $\times$ *Z. mays* ssp. *mexicana* crosses reporting improved characters like more number of tillers, increased height, increased 100 seed weight and resistance to lodging. Further, CV noted for plant height was high (40.10%), indicating the higher variation in the population can be useful for the improvement in plant height and may be this trait can further be used for the fodder purpose and despite of the low density plant population, can enhance the yield (Aldrich *et al.*, 1986).

Number of brace roots

Teosinte possesses profuse brace roots as compared to maize probably because the trait being one of the adaptive traits for survival and support. In the investigation, teosinte showed more number of brace roots (21.2) than the maize inbreds, however it varies according to the season. In the present investigation, it was noted that, teosinte carries brace roots more than one nodes while after hybridisation, the F_s were also observed for profuse aerial roots even more in number than teosinte. While the inbred maize lines showed variation for the trait from minimum of 4.2 in CML-451 to maximum of 16.0 in CAL-1444, in F₁ it was ranged from minimum 19.6 (CIII) to 47.2 (CI). Similar results were reported by Taramino *et al.* (2007) and Zhang *et al.* (2018). They reported the expression of *ZmRTCS* genes and control of flowering time gene in the brace root developments in the teosinte introgressed F_s, respectively. The higher CV (65.82%) for the trait can be inferred as the variability was created by the introgression of teosinte alleles in to maize inbred lines and can be utilised in maize breeding for improvement of stem anchorage, lodging resistance, nitrogen fixation and uptakes, and oxygen supply etc.

Kernel traits

Seed size had significant effect on ear diameter, ear length, number of kernels per ear, ear weight, 1000-kernel weight, hectolitre weight and grain yield of corn (Kara, 2011). Among the kernel traits highest coefficient of variation was observed in KWT (34.76%) followed by L/W ratio (28.91%) and FFD (20.83%). Hence these characters have great prospects in maize breeding and these can further be partitioned in to phenotypic, genotypic and environmental components for critical insight into different component of variance. F_s were

Table 2: Estimates of variability parameters for kernel traits of parental and F₁ plants

	KW(cm)	KL(cm)	Area (cm ²)	Perimeter(cm)	L/W	Roundness	FFD(g/cm ²)	KWT(g)
PARENTS								
Teosinte	0.37	0.73	0.24	2.03	1.93	0.53	223.07	60.25
CAL 1444	0.67	0.75	0.45	2.53	1.11	0.84	425.33	213.73
CAL 159	0.70	0.68	0.37	2.33	0.96	0.87	368.82	175.56
CML 451	0.75	0.77	0.47	2.57	1.02	0.88	475.24	274.45
F₁ HYBRIDS								
CI	0.61	0.78	0.35	2.32	1.27	0.79	414.52	197.23
CII	0.69	0.71	0.37	2.33	1.02	0.89	361.34	177.02
CIII	0.74	0.75	0.40	2.46	1.00	0.87	385.14	213.75
Range	0.37-0.75	0.68-0.78	0.24-0.47	2.03-2.57	0.96-1.93	0.53-0.89	223.07-475.24	60.25-274.45
Mean	.647	.738	.376	2.367	1.187	.810	379.065	187.427
Variance	.017	.001	.006	.032	.118	.016	6239.603	4246.162
C.V. (%)	20.20	4.71	19.91	7.61	28.91	15.79	20.83	34.76
Std. Error mean	.0494	.0132	.0285	.0681	.130	.048	29.855	24.629
Skewness	-2.006	-.660	-.843	-.998	2.205	-2.301	-1.311	-1.150
Kurtosis	4.345	-.211	1.331	1.408	5.017	5.468	2.799	2.881

*KW= kernel width, KL=kernel length, L/W=length width ratio, FFD= Factor form density, KWT= 1000-kernel weight

Table 3: Estimates of Pearson's correlation coefficient among different traits

	DA	DS	Number of tillers and main stalk	Plant height (cm)	Number of brace roots	KW	KL (cm)	Area (cm ²)	Perimeter	L/W	Roundness	FFD	KWT (g)
DA	1	.985**	.512	.643	-.130	-.905**	-.028	-.679	-.703	.935**	-.950**	-.755*	-.764*
DS		1	.380	.572	-.186	-.858*	.044	-.601	-.616	.900**	-.924**	-.674	-.687
Number of tillers and main stalk			1	.868*	.524	-.719	-.111	-.820*	-.812*	.698	-.658	-.788*	-.770*
Plant height (cm)				1	.379	-.774*	-.054	-.898**	-.857*	.787*	-.788*	-.853*	-.806*
Number of brace roots					1	-.284	.269	-.424	-.372	.224	-.170	-.154	-.252
KW						1	.039	.874*	.883**	-.982**	.981**	.841*	.896**
KL (cm)							1	.297	.357	.096	-.037	.456	.428
Area (cm ²)								1	.992**	-.816*	.830*	.926**	.948**
Perimeter									1	-.818*	.830*	.931**	.960**
L/W										1	-.994**	-.789*	-.825*
Roundness											1	.815*	.846*
FFD												1	.979**
KWT (g)													1

**Correlation is significant at the 0.01 level (2-tailed). *Correlation is significant at the 0.05 level (2-tailed). KW-Kernel width, KL-kernel length, L/W-length width ratio, FFD-Factor form density, KWT-1000 kernel weight.



Fig.1: Agro-morphological traits taken for observation in Teosinte and the introgressed F₁s from the experimental field: a) Tillering habit in Teosinte plant (b) Tillering habit in F₁ plants of C-II (CAL-159 × Teosinte) c) F₁ hybrids of C-III (CML-451 × Teosinte) with tall plant height d) Brace roots development in the F₁ hybrids.

intermediate of both the parents for all the kernel traits. Among the parental lines for all the kernel traits teosinte has the lowest value, that is the area, perimeter occupied by it is very less and it is the least round (0.53) and more cylindrical with least FFD value (223.07 g/cm³), and least KWT (60.25 g) however, the L/W ratio of teosinte is the highest (1.93). The maize inbred CML-451 showed highest value for other traits, along with KWT (274.45g) hence can be utilised further for evaluating yield and ear traits as seed size had significant effect on ear diameter, ear length, number of kernels per ear, ear weight, 1000-kernel weight, and grain yield of corn (Kara, 2011). Kernels of CML-451 are being more round (0.89) have the highest FFD (475.24 g/cm³) value. As compared to the parent inbred CAL-159, F₁ of C-II is more round as roundness is 0.896 and FFD is 361.34g/cm³ and increased L/W (1.02) but has however smaller size (KL, KW) than the parent. F₁ of CI has more L/W ratio (1.27 cm) due to increased length and decreased width, less roundness (0.797) and decreased 1000-seed weight (197.23g) as compared to the parental inbred CAL-1444. As compared to the parent inbred CML-451, F₁ of C-III is lesser for every trait than the parent. Decreased KWT in the F₁ hybrids than parental maize inbreds showed that the impact of teosinte pollen somewhere exists. So the teosinte introgression creates a huge variation in the kernel traits detail multi-location evaluation is required to quantify the heritable and non-heritable variance. Liu *et al.* (2016a, b) and Karn *et al.* (2017) also reported teosinte alien gene introgression in maize accomplished for improvement of several quantitative traits like kernel composition, kernel weight, kernel row number (KRN), kernel area and kernel length using hybridization.

Correlation analysis

Simple Pearson's correlation analysis showed that all the agro-morphological traits were negatively associated with 1000- seed weight, whereas all the kernel traits showed significant positive correlation with 1000-kernel weight except KL (0.428) (Table 3). The kernel L/W ratio

was significantly negatively associated with 1000-seed weight (-0.827). Similar findings were observed by Liu *et al.* (2016b). The positive correlation coefficient with KWT is highest for FFD (0.979) followed by kernel perimeter (0.960). KW has significant and positive association with all the traits except KL (0.045) and significant negative association with L/W ratio. The KL showed non-significant positive association with all the traits; however with roundness it was negatively associated. Kernel area and kernel perimeter had positively and significantly correlated with all the traits except KL and L/W ratio. Kernel L/W ratio has significant negative association with all the traits except KL. Kernel roundness has negative association with KL and L/W ratio. FFD is significantly and positively correlated with all the traits except KL (0.456) and significantly negatively associated with L/W ratio (-0.789). The correlation coefficient analysis is useful in identifying the component traits in a population that is different from the normal maize population which can be used for yield improvement. These associations quantify the possibility of indirect selection gains in correlated traits hence; the kernel traits being positively associated can improvise the 1000-kernel weight which is an important yield contributing trait.

Skewness and kurtosis

The positive skewness for all the morphological traits showed the preponderance of complementary gene interactions on the traits which need intensive selection for rapid gain. While DA and DS had leptokurtic curve (under control of relatively few segregating genes and narrow variability), all the other agro-morphological traits showed platykurtic kurtosis, hence can be said to be controlled by many genes having wider variability and large diversity. Almost all the kernel traits showed a negative skewness except L/W ratio which indicated effective mild selection for rapid genetic gain along with the governance of duplicate epistasis gene action. This showed corroboration with the findings of Adhikari *et al.* (2020). Platykurtic nature kurtosis for the trait KL, kernel area, perimeter, FFD and KWT indicates existence of high variability in these traits.

CONCLUSION

The present investigation aimed to observe the variation created by introgression of wild teosinte into the maize inbred lines in some of the novel traits. Though the study is preliminary in nature yet has generated many valuable information and also indicated great prospects of teosinte in maize germplasm enhancement and improvement. In this study, number of tillers and main stalk, number of brace roots, plant height showed high variability along with the seed kernel traits namely kernel weight, FFD, kernel area which can be used for exploiting the variation and selection for the traits that will lead to maize



Fig. 2: Teosinte seeds for analysis in ImageJ for kernel traits

improvement. Further, introgression of teosinte alleles resulted to create higher magnitude of variation in different maize population, so exploitation of these predomestication alleles can expand the genetic resource of maize. However, high CV (>20%) may be the resultant of inherent genotypic variability as well experimental variability. So for accuracy, measures should be taken to reduce the experimental variability. From skewness and kurtosis analysis, intensive selection was recommended for the morphological traits while mild selection for most of the kernel traits. The kernel traits which showed significantly positive association with the 1000- kernel weight can be partitioned to phenotypic, genotypic and environmental correlation coefficient so that the cause of association precisely is known whether it is due to common biochemical pathways of two traits or the linkage relationship. Hence the existing variability in teosinte and the combined effort of modern plant breeding with its improved tools like quantitative trait loci (QTL) mapping, single nucleotide polymorphism (SNP) genotyping, nested associated mapping (NAM) will be helpful in exploring useful variability and translating them into the improvement of various traits.

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Received: March 27 2021

Accepted: April 28, 2021