Seasonal influence, heat unit accumulation and heat use efficiency in relation to maize grain yield in Pakistan

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Abstract

Variations in ambient temperature affect crop yield by modifying the duration of phenological phases and physiological processes. An experimental study was carried out at the Maize and Millets Research Institute (MMRI), Yusafwala, Sahiwal, Pakistan, to determine the seasonal effects of temperature on indigenous and exotic maize (*Zea mays* L.) hybrids based on morphological, phenological, physiological and grain quality traits in four different growing seasons: kharif 2016 and 2017, and spring 2017 and 2018. Seven indigenous and three exotic hybrids were sown in a randomized complete block design with a split plot arrangement, in three replications. Significant differences between hybrids and growing seasons were found for grain yield, related traits and temperature indices (cumulative heat units, photothermal index and heat use efficiency). Correlation analysis disclosed a significant positive relationship between grain yield and net photosynthetic rate (0.854, $P \leq 0.01$), number of grains per ear (0.624, $P \leq 0.01$) and heat use efficiency (0.980, $P \leq 0.01$) in spring seasons. During kharif, net photosynthetic rate (0.675, $P \leq 0.01$) and heat use efficiency (0.996, $P \leq 0.01$) contributed significantly to grain yield, whereas number of grains per ear (−0.146, not significant) had no significant impact on grain yield. Cumulative heat units and heat use efficiency resulted the temperature indices with the greatest influence on grain yield, and should be considered during the selection of parents to develop high-yielding, climate-smart maize hybrids. Indigenous maize hybrids showed higher yields and were more heat tolerant than exotic hybrids, and the spring sowing season appeared to be the most suitable for the cultivation of maize crops.

Introduction

Maize (*Zea mays* L.) is a tropical zone crop now also widely cultivated in temperate zones. As a C_4 plant, it can withstand higher temperatures than C_3 crops such as rice and wheat. The huge variability of maize germplasm based on geographic location, morphological characteristics and habitat makes it one of the most widely used crops, grown in areas extending from very hot regions in Sub-Saharan Africa and South Asia to very cold regions in eastern Canada. The third most important cereal crop worldwide after wheat and rice, it is cultivated on a total area of 197.19 million hectares with a total production of 1134.75 million metric tons and an average yield of 5.75 metric tons per hectare (FAO, 2017). Predominantly, it is grown for poultry & livestock feed (65%) and human consumption (35%) (Halidu et al., 2014). However, it also serves as a source of raw material for the production of many industrial products such as starch, oil, protein, alcoholic beverages, foods, sweeteners, cosmetics and bio-fuel etc (Serna-Saldivar, 2019). About 208 million people in Sub-Saharan Africa depend directly on maize as a principal source of food and livelihood (Macauley, 2015). In Pakistan, maize is the third most important cereal crop after wheat and rice. It was grown on an area of 1.229 million hectares with the total production of 5.702 million tons with an average yield of 4.640 tons' ha^{-1} (Govt. of Pakistan, 2018-19). Maize is primarily used as feed and fodder for poultry and livestock industry, respectively. Furthermore, its uses in wet milling industry is also increasing day-by-day due to its increasing demand as food byproducts such as food sweetener and snakes etc. Maize oil is also being used in cooking industry for the manufacturing of vegetable ghee and cooking oil. However, a small proportion of maize production is also directly utilized by human as roasted grains or cobs.

Temperature is one of the most important environmental factors that regulates the rate of plant growth and development. Plant species respond differently under changing climatic and environmental conditions. Even different varieties of the same species have varying responses across different regions, with no exception to maize. All morpho-physiological and phenological development in plants is markedly influenced by temperature. Different maize hybrids, due to their high variability and wide adaptability, require different numbers of cumulative heat units (CHUs) or growing degree days (GDDs) for growth, development and maturity. Different planting seasons can lead to different environmental conditions from emergence to physiological maturity in relation to temperature intensity, day length and number of days required for crop maturity. The most common temperature indexes used to estimate the rate of plant development are GDD or CHU; other temperature indexes include photothermal index (PTI), heat use efficiency (HUE), photothermal unit (PTU) and heliothermal unit (HTU) are also used for estimation of crop maturity patterns. The accumulation of CHUs determines crop maturity and yield, and yield components under given environmental conditions. Sur and Sharma (1999) reported that delayed planting can reduce total CHU due to lower temperatures experienced by late sown crops during the seed-filling period. However, Beard and Geng (1982) found that lower yields in late-planted crops were generally associated with higher temperatures during the early growth period, which promotes excessive early stem growth. A wide range of maize cultivars characterized by early, medium and late maturity is available, and each cultivar has specific GDD requirements ranging from 1800 to 3700 at a base temperature of 10°C (FAO, 2018).

In Pakistan, maize is planted in two seasons: kharif (autumn) and spring. It is mainly grown in Punjab and Khyber Pakhtunkhwa provinces of Pakistan, Punjab being the highest shareholder in production (above 85%). In Punjab, Spring maize is sown under low temperature conditions in the months of January and February, and the vegetative growth phase thus takes place at a range of low to medium temperatures in February and March. However, the reproductive stage of spring-sown maize occurs at high temperatures in May, and the crop is harvested under high temperature conditions in June and July. In contrast to spring maize, autumn maize is sown under high temperature and high humidity conditions in July and August. It completes its vegetative stage at high to medium temperatures from September to October before entering the reproductive phase while it matures and harvested at low temperatures in December. Spring maize matures 10 to 15 days earlier than kharif maize due to the presence of high temperature during and after the grain-filling stage (Ahmad et al., 2018). Thus, two opposite sets of environmental conditions prevail from germination to maturity in spring and kharif maize crops.

Temperature variations in the field can be achieved by planting crops at different seasons and sowing dates, so that the crop will grow under different conditions of temperature, hours of sunshine, day length and relative humidity. The present study was designed to investigate the relationship of CHU with grain yield and associated morphological, physiological, phenological and grain quality components in different indigenous and exotic maize hybrids. In addition, heat use and seasonal efficiency were compared between indigenous and exotic hybrids sown in four consecutive growing seasons (kharif, 2016 and 2017; spring, 2017 and 2018).

Materials and Methods

Experimental site

Field experiments were conducted in four consecutive maize growing seasons: Kharif 2016 (August-December), Spring 2017 (February-June), Kharif 2017 (August-December) and Spring 2018 (February-June) at rese-

Table 1 - Origin of Indigenous (1-7) and Exotic (8-10) maize hybrids used in the study.

Kharif sown hybrids			Spring sown hybrids		
Sr.	Hybrid	Origin	Sr.	Hybrid	Origin
1	YH-5482	MMRI, Yusafwala	1	YH-5482	MMRI, Yusafwala
2	YH-5427	MMRI, Yusafwala	2	YH-5427	MMRI, Yusafwala
3	YH-5507	MMRI, Yusafwala	3	YH-5507	MMRI, Yusafwala
4	YH-5532	MMRI, Yusafwala	4	YH-5532	MMRI, Yusafwala
5	YH-1898	MMRI, Yusafwala	5	YH-1898	MMRI, Yusafwala
6	FH-949	MRS, AARI, Faisalabad	6	FH-949	MRS, AARI, Faisalabad
7	FH-1046	MRS, AARI, Faisalabad	7	FH-1046	MRS, AARI, Faisalabad
8	NT-6621	Syngenta, Pakistan	8	DK-9108	Monsanto, Pakistan
9	DK-6789	Monsanto, Pakistan	9	P-1543	Pioneer, Pakistan
10	Dk-6714	Monsanto, Pakistan	10	DK-6724	Monsanto, Pakistan

MMRI, Yusafwala = Maize and Millets Research Institute, Yusafwala, Sahiwal, Pakistan, MRS, AARI, Faisalabad = Maize Research Station, Ayub Agricultural Research Institute, Faisalabad arch fields of the Maize and Millets Research Institute (MMRI), Yusafwala Sahiwal, Pakistan. The experimental site was located at 30.68°N latitude, 73.21°E longitude at an altitude of 172 m above mean sea level. The soil type at the experimental site was clay loam with alkaline pH in all four seasons.

Experimental materials and Layout design

Seven indigenous and three exotic maize hybrids were sown in a randomized complete block design with a split plot arrangement and three replications in all seasons (Table 1). Kharif-sown exotic maize hybrids differed from spring-sown hybrids in their season specificity. Indigenous hybrids were the same in both kharif and spring seasons. Hybrids were sown in the 3rd week of August for kharif sowing or the 3rd week of February for spring sowing in both seasons (2016-17 and 2017-18) with the help of a dibbler at 2 seeds per hill. The plant-to-plant distance was 20 cm and row-to-row distance was 75 cm, and net plot size was 5 m × 3 m. Thinning was done at the 3-4 leaf stage to ensure optimum plant populations. Standard agronomic and plant protection measures were applied for all treatments.

Data acquisition

At maturity, the two central rows were harvested in the 2nd week of December for kharif crops and the 1st week of June for spring crops. Grain yield per plot was calculated for every entry from fresh ear weight per plot (adjusted for 15% grain moisture) using the following formula (Mafouasson et al., 2017):

$$\text{Grain yield (kg ha}^{-1}\text{)} = \frac{\text{Fresh ear weight (kg/plot)}\times(100-\ )\times 0.8\times 10000}{(100-15)\times\text{Area harvested/Plot}}$$

The number of grains per ear (NGE) was counted in 10 random ears from each entry. Grain protein percentage was estimated with near infrared spectroscopy (Inframatic 9200; Perten Instruments, Sweden). The physiological parameter photosynthesis rate (µmole $m^{-2}\cdot s^{-1}$) was measured during the grain filling stage in 10 random ear leaves per hybrid between 9:30 a.m. and 11:30 a.m. with an infrared gas analyzer (Model CI-340, CID Bio-Science, USA). Days to maturity were calculated by counting days from the date of sowing to the date of physiological maturity. Metrological data were obtained from a radio-controlled weather station installed at MMRI. The different heat units were calculated as follows:

$$GDD = \sum_{i=0}^{n} \left[\frac{(\text{Tmax} - \text{Tmin})}{2} - \text{Tbase}\right] \quad \text{(Thavaprakaash, 2007)}$$

$$\text{HUE} = \text{Grain yield} \div \text{GDD} \quad \text{(Haider et al., 2003)}$$

$$\text{PTI} = \text{GDD} \div \text{Growing days} \quad \text{(Haider et al., 2003)}$$

$$\text{Seasonal efficiency} = \frac{\text{(Yield in a given season}}{\text{Mean yield in all seasons)}} \times 100$$

(Thavapprakaash et al., 2007)

Biometrical analysis

The data were compared with analysis of variance and post-hoc tests (Kwon & Torrie, 1964) to detect differences among maize hybrids, seasons and their interactions. Correlation analysis was also done to determine the relationships between different grain yields and different plant traits along with temperature indices (Steel & Torrie, 1980). The XLSTAT 16.0 and Statistix 16.0 statistical applications were used for statistical analyses, and Microsoft Excel was used to create graphs for data presentation.

Meteorological conditions

Meteorological data showed that spring-sown maize hybrids experienced average maximum temperatures of 43.2°C in 2017 and 40.8°C in 2018 (Fig. 1). Kharif-sown maize crops experienced maximum temperatures of 37.2°C in 2016 and 38.0°C in 2017, although

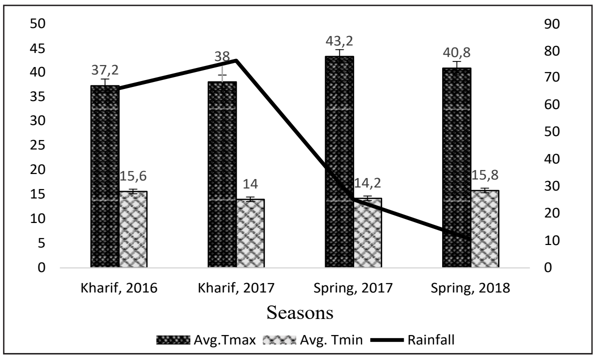

Fig. 1- Meteorological data for maize growing seasons from Kharif 2016 to Spring 2018.

the average maximum temperatures in kharif seasons were lower than in both spring seasons. Spring-sown maize crops experienced severe heat stress during the reproductive phase (≥46°C in spring 2017 and ≥43°C in spring 2018), with much higher temperatures than needed for optimum growth and development (35°C) during the reproductive phase (Table 2). In contrast to average maximum temperatures, average minimum temperatures were highest in spring 2018 (15.8°C) followed by kharif 2016 (15.6°C). However, the differences between seasons in average minimum temperature were small. Precipitation was greater during kharif seasons (75.2 mm) than during spring seasons (19.6 mm) (Table 2).

Table 2 - Mean minimum and maximum temperature and rainfall recorded during Kharif 2016, 2017 and Spring 2017, 2018.

Month/Year	Temperature (°C)			Rainfall (mm)
	Max.	Min.	Mean	
Kharif, 2016				
18 Aug	41	24	32.4	65
September	41	22	31.7	1
October	39	14	27.2	0
November	33	9	20.8	0
08 Dec	32	9	19.4	0
Spring, 2017				
17 Feb	33	7	20.4	0
March	43	7	23.2	1
April	47	13	30.9	8.5
May	48	20	33.9	16.6
02 Jun	45	24	34.3	0
Kharif, 2017				
18 Aug	43	24	32.9	9
September	42	20	31.1	74
October	41	15	28.6	0
November	32	7	20.2	2.2
08 Dec	32	4	18.1	0
Spring, 2018				
17 Feb	32	9	20.9	0
March	40	14	25.4	6.6
April	46	19	30.4	3.5
20 May	45	21	31.9	4

Results and discussion

Meteorological conditions

Several environmental factors such as temperature, humidity, light intensity and rainfall play an important role in plant growth and development. However, temperature is thought to be the most critical factor (Wahid et al., 2007). In the present study, meteorological data i.e. temperature, humidity, rainfall etc. showed that maize hybrids sown during the kharif seasons were exposed to higher temperatures during the vegetative phase, whereas in those sown during the spring seasons, the highest temperatures were recorded during the reproductive phase. Similar results were also found by different researchers who showed that reproductive phase of spring sown maize was the most vulnerable phase to heat stress and could cause sufficient losses to grain yield (Yousaf et al., 2017; Yousaf et al., 2018, Aamer et al., 2018). Furthermore, kharif-sown maize received sufficient rainfall during the early vegetative phase, which may have helped the crop to sustain growth during high temperature periods.

Analysis of variance and post-hoc multiple comparison test

The results of combined analysis of variance showed that the maize hybrids differed significantly for all traits studied (Table 3). In addition, significant differences between seasons were found for all traits. However, some plant traits such as net photosynthetic rate and number of grains per ear (NGE) showed no significant differences between kharif seasons but significant differences between spring seasons. Net photosynthetic rate was highest in the indigenous hybrid YH-5507 (26.5 μmol·m-2·s^{-1}) followed by DK-9108 (23.0 μmol·m^{-2}·s^{-1}), and was lowest in the exotic hybrid P-1543 (17.0 μmol·m^{-2}·s^{-1}) under spring seasons. Similarly, the indigenous hybrid FH-949 produced the highest NGE (721) in the spring seasons, followed by the exotic hybrid DK-9108 (683), while the lowest NGE (546) was recorded in the exotic hybrid P-1543. The number of grains per ear is also a key trait which is severely affected by high temperatures. In the present study, NGE showed a strong positive correlation with grain yield, but only in spring seasons; this finding suggests that NGE could be used as a selection criterion for the development of heat-tolerant maize hybrids, as suggested by Khodarahmpour (2012). Similar findings were revealed by Yousaf et al. (2018) stating the presence of highly significant differences among indigenous and exotic maize hybrids for grain yield and quality-related traits under spring sowning condition.

Maize, being a C4 crop, utilizes temperature efficiently and produces its food in the presence of adequate sunlight and temperature. However, high temperatures can impair plant growth by reducing photosynthetic capacity as a result of inhibited RuBisCO activity

Table 3 - Combined analysis of variance (ANOVA) for plant traits, temperature indices and grain yield in maize hybrids.

Source	DF	Pn	NGE	Protein	DM	PTI	HUE	CHU	GY
Replication (R)	1	111.02	39754.2	13.1105	3764.8	41.36	3.9653	16498	7953586
Seasons (S)	10	82.5**	59100**	6.86**	1293.2**	20.6**	13.9**	35649.1**	35500000**
Error (R × S)	10	0.16	1113.1	0.089	8.91	0.230	0.0084	39.7	20226.8
Hybrids (H)	8	80.31**	11374.3**	2.029**	13.16**	0.054**	0.995**	3062**	3689965**
Interaction (S × H)	80	37.39**	9054**	0.977**	16.08**	0.052**	0.8125**	3433.5**	2794978**
Error (R × S × H)	88	0.000992	78.6	0.00011	0.01	0.0005	0.0014	0.6	5243.34

* Significant at P≤0.05, ** Significant at P≤0.01, NS = Nonsignificant Pn = Photosynthetic rate (μmol m-2 s^{-1}), NGE = Number of grains per ear, Protein = Grain protein percentage (%), DM = Days to maturity, CHU = Cumulative heat units, HUE = Heat use efficiency, PTI = Photothermal index, GY = Grain yield per hectare (kg ha^{-1})

Table 4 - Grain yield, yield components and temperature indices of maize hybrids during Kharif, 2016 and 2017.

Sr. No	Hybrid	Pn	NGE	Protein	DM	PTI	HUE	CHU	GY
1	YH-5482	25.4 a	591 a	14.3 a	110 abcd	17.15 abcd	5.105 a	1877 abcd	9582 a
2	YH-5427	25.4 a	580 a	14.3 a	108 cd	17.26 ab	4.945 ab	1864 cd	9212 ab
3	YH-5507	24.9 a	545 a	14.4 a	107 d	17.33 a	4.94 ab	1854 d	9164 ab
4	YH-5532	25.1 a	596 a	14.3 a	111 ab	17.04 cd	4.615 abc	1892 ab	8728 abc
5	YH-1898	21.4 a	550 a	14.5 a	111 abc	17.07 bcd	4.775 ab	1887 abc	9008 ab
6	FH-949	19.0 a	591 a	14.4 a	109 bcd	17.21 abc	3.84 c	1867 cd	7165 c
7	FH-1046	21.8 a	574 a	14.0 ab	109 bcd	17.19 abc	4.205 bc	1874 bcd	7878 bc
8	NT-6621	22.6 a	520 a	13.6 b	112 a	16.95 d	4.525 abc	1899 a	8585 abc
9	DK-6789	20.3 a	531 a	13.7 b	110 abc	17.08 bcd	4.58 abc	1879 abc	8600 abc
10	Dk-6714	19.4 a	519 a	13.7 b	111 abc	17.06 cd	4.67 abc	1885 abc	8800 ab
Tukey (p≤0.05)		7.56	137.24	0.55	2.59	0.1998	0.8368	24.709	1617.8

Pn = Photosynthetic rate (μmol m^{-2} s^{-1}), NGE = Number of grains per ear, Protein = Grain protein percentage (%), DM = Days to maturity, CHU = Cumulative heat units, HUE = Heat use efficiency, PTI = Photothermal index, GY = Grain yield per hectare (kg ha^{-1})

(Salvucci & Crafts-Brandner, 2004). In the present study, hybrids differed significantly in net photosynthetic rate, which was highest in indigenous hybrids YH-5482 and YH-5427 sown in kharif, and in hybrids YH-5507 and YH-1898 sown in spring. However, the photosynthetic activity of spring seasons was lower than in kharif seasons. This may be due to the higher temperatures (≥46°C) during the late vegetative and early flowering stages in spring. Sinsawat et al. (2004) found that high temperatures (≥45°C) for 96 hours drastically reduced photosynthetic activity by damaging the photosynthetic apparatus and inactivating RuBisCO. Significant differences among maize hybrids for CHU in the present study reflected differences in maturity.

The indigenous hybrids differed significantly from exotic hybrids in grain protein percentage during kharif seasons (Table 4). The differences between indigenous and exotic hybrid groups were significant while intra group differences were negligible except for YH-1046, which showed a nonsignificant difference with both groups. The indigenous hybrid YH-1898 had the highest grain protein percentage (14.5%), and similar values were observed in all other indigenous hybrids, although the values differed significantly compared to exotic hybrids. The lowest grain protein percentage was observed in the exotic hybrid NT-6621 (13.6%), and similar values were seen in hybrids DK-67 (13.7%), DK-6789 (13.7%) and FH-1046 (14.0%). The data showed that the differences between the hybrids during the spring seasons were also statistically significant, with an approximately similar pattern: the indigenous hybrid YH-1898 again had the highest grain protein percentage (14.5%) while the exotic hybrid DK-6724 had the lowest value for this trait (12.2%). Overall, grain protein percentage was higher in kharif seasons than in spring seasons. Wilhelm et al. (1999) also found that grain quality parameters such as protein, starch and oil content were reduced by high temperatures due to the disruption of associated proteins and breakdown of starch molecules to low molecular weight sugars. The indigenous hybrids tested here showed better performance than the exotic hybrids for grain protein percentage. Similar results were reported by Yousaf et al. (2018), who also found that indigenous hybrids were superior to exotic hybrids in terms of grain quality, especially grain protein percentage.

Days to maturity is also considered one of the main factors contributing to grain yield. In the present study, maize hybrids differed considerably in days to maturity. The data presented in Table 4 shows significant differences among hybrids for days to maturity (DM) in both kharif and spring seasons. However, kharif-sown hybrids needed more days to attain its physiological maturity as compared to spring-sown hybrids. The longest time (in days) to maturity was observed in exotic hybrid NT-6621 (112 days) while the shortest time was observed in the indigenous hybrid YH-5507 (107 days) in kharif seasons. However, in spring seasons, FH-1046 and P-1543 had the shortest times to maturity (96 days) while YH-5507 had the longest time (102 days). The results of current study unveiled that hybrids grown during kharif seasons took approximately 10 days longer to mature than in spring seasons. In the latter sowing periods, days to maturity was positively associated with grain yield as found by Ahmad et al. (2011) who showed that more the days taken to maturity, more will be the grain yield in kharif sown maize crop. Similarly, Long et al. (2017) also described the role of planting dates and maturity of hybrids with grain yield in maize and concluded that the hybrids having longer reproductive stage are comparatively more productive.

Temperature indices are used to quantify crop plant parameters related to tolerance, physiological efficiency and grain yield. The most important of these indices

Table 5 - Grain yield, yield components and temperature indices of maize hybrids during Spring 2017 and 2018.

Sr. No	Hybrid	Pn	NGE	Protein	DM	PTI	HUE	CHU	GY
1	YH-5482	20.5abc	617 abcd	13.8 ab	97 ab	18.53 ab	5.40 abc	1788 b	9652 bc
2	YH-5427	20.5 abc	578 cd	13.9 ab	98 ab	18.50 ab	5.35 abc	1813 ab	9708 abc
3	YH-5507	26.5 a	662 abc	13.4 ab	102 a	18.51 ab	6.21 a	1888 a	11705 a
4	YH-5532	15.5 bc	609 bcd	12.4 b	100 ab	18.57 ab	4.56 c	1857 ab	8461 c
5	YH-1898	23.5 ab	598 bcd	14.5 a	100 ab	18.40 b	5.58 abc	1840 ab	10268 abc
6	FH-949	17.5 bc	721 a	13.1 ab	99 ab	18.60 ab	5.66 abc	1833 ab	10347 abc
7	FH-1046	21.0 abc	658 abc	13.5 ab	96 b	18.62 ab	5.90 ab	1788 b	10545 ab
8	DK-9108	23.0 abc	683 ab	13.4 ab	98 ab	18.53 ab	5.70 abc	1807 ab	10292 abc
9	P-1543	15.0 c	546 d	13.7 ab	96 b	18.63 ab	4.87 bc	1789 b	8658 bc
10	DK-6724	17.5 bc	636 abcd	12.2 b	98 ab	18.73 a	5.37 abc	1827 ab	9746 abc
Tukey ($p \leq 0.05$)		8.17	104.92	1.588	5.995	0.32	1.195	96.73	2032.0

Pn = Photosynthetic rate (µmol x m^{-2} x s^{-1}), NGE = Number of grains per ear, Protein = Grain protein percentage (%),
DM = Days to maturity, CHU = Cumulative heat units, HUE = Heat use efficiency, PTI = Photothermal index, GY = Grain yield per hectare (kg x ha^{-1})

are PTI index, HUE and CHU. As seen for morphological, physiological and phenological traits, maize hybrids also differed significantly in the different temperature indices analyzed in this study. Photothermal index (PTI) or heat units required to progress from one stage to the next differed among maize hybrids in both kharif and spring seasons (Tables 4 and 5). However, PTI values were higher during spring seasons compared to kharif seasons, because the time (in days) required to attain successive phenological phases was shorter in spring due to higher temperatures, and this allowed the plants to accumulate more heat units per growth stage. In kharif seasons, PTI was highest in the indigenous hybrid YH-5507 (17.33) and lowest in hybrid NT-6621 (16.95). In spring seasons, PTI was highest in the exotic hybrid DK-6724 (18.73) while YH-1898 took minimum heat units to pass from one phenophases to other (18.40) followed by YH-5427 (18.50) (Table 5). Thavaprakaash et al. (2007) also found higher PTI values in the spring season compared to kharif season in maize. One possible reason for the higher PTI is because plants need to accumulate more GDD in fewer days. However, PTI in the present study showed a negative relationship with grain yield in spring-sown hybrids due to the shorter time available for reserves to accumulate in ears. Heat use efficiency, which can be defined as the grain yield obtained per degree day, is one of the most important temperature indices, and also differed among maize hybrids in both seasons (Tables 4 and 5). During kharif, the indigenous hybrid YH-5482 had the highest HUE (5.105 kg/GDD), while the indigenous hybrid FH-949 had the lowest HUE (3.84 kg/GDD). Heat use efficiency among kharif-sown hybrids was lower compared to spring seasons (Fig. 2). In spring seasons, maximum HUE was observed in hybrid YH-5507 (6.21 kg/GDD) and the lowest HUE in hybrid YH-5532 (4.56 kg/GDD) (Table 5). Higher HUE values in spring sown crop were due to the higher grain yield and slightly lower CHU values in spring seasons. These results exemplify the strong correlation between grain yield and HUE, as confirmed by correlation coefficient analysis. Moreover, this association was strong in both kharif and spring seasons as shown by Thavaprakaash et al. (2007) in baby corn who found a strong positive association between grain yield and HUE.

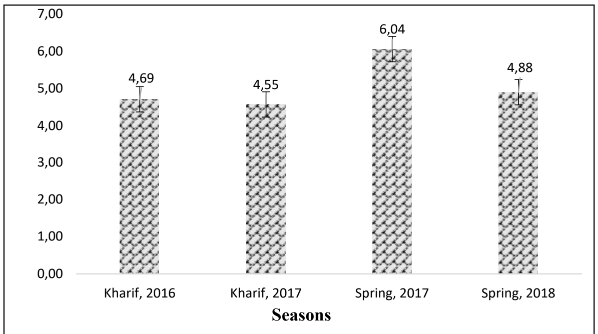

Fig. 2 - Heat use efficiency in different growing seasons.

Cumulative heat units, another important temperature index, is thought to be highly associated with grain yield in maize. During kharif seasons, the exotic maize hybrid NT-6621 had the highest CHU (1899) while the indigenous maize hybrid YH-5407 had the lowest CHU (1854) (Table 4). During both spring seasons (2017 and 2018), hybrid YH-5507 had the highest CHU (1888) while hybrids YH-5482 and FH-1046 had the lowest CHU (1788) (Table 5). Overall heat unit accumulation was higher in kharif seasons than in spring seasons due to higher temperatures during the early development stages in kharif-sown hybrids, and to the prolonged growing periods. Higher CHUs in maize hybrids during the kharif seasons illustrated that kharif-sown crops required more days to mature than spring-sown hybrids. Higher temperatures during grain filling and maturation in the spring seasons may have limited grain yield

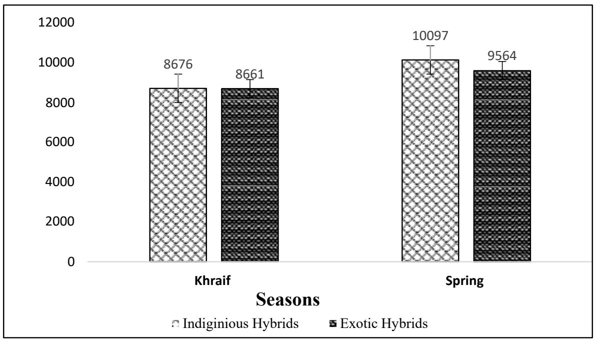

Fig. 3 - Comparison of indigenous and exotic maize hybrids for grain yield per hectare.

and related traits by disrupting photosynthetic activity.

Maize hybrids also differed significantly in grain yield in both kharif and spring seasons. During kharif seasons, the indigenous maize hybrid YH-5482 produced the highest grain yield (9582 kg/ha) followed by another indigenous hybrid, YH-5427 (9512 kg/ha), while the lowest grain yield was produced by hybrid FH-949 (7165 kg/ha) (Table 4). During both spring seasons, the indigenous hybrid YH-5507 had the highest grain yield (11705 kg/ha) followed by FH-1046 (10545 kg/ha) and FH-949 (10347 kg/ha), while the lowest grain yield was seen in the indigenous hybrid YH-5432 (8461 kg/ha) (Table 5). Overall, grain yield was higher in spring seasons than in kharif seasons. In addition, grain yield in kharif seasons was nonsignificantly higher in exotic hybrids. However, the grain yield in spring seasons was significantly higher among indigenous hybrids (540 kg ha^{-1}) than exotic hybrids (Fig. 3). Grain yield is the product of the combined effects of all yield components under a specific set of environmental conditions. Maize hybrids sown in the kharif and spring seasons differed considerably in grain yield. The differences within the same hybrid sown in different seasons may be attributed to the interactive effects of several environmental variables. Results of current study were in line with findings reported by Thavaprakaash et al. (2007), who also found significant differences among maize hybrids for grain yield under variable environmental conditions. Grain yield in spring-sown maize hybrids was higher than when they were sown in kharif seasons. The difference may be due to the higher HUE and NGE, which contributed positively to improved grain yield. Furthermore, average minimum temperature during the grain filling and maturation stages in the kharif seasons was below the base temperature (10°C), and this factor can severely reduce grain yield by inhibiting vital physiological functions such as photosynthesis, stem reserve mobilization, assimilate portioning, grain filling rate and harvest index. Moreover, indigenous maize hybrids were more productive under spring season conditions. The likely reason for this difference is that the indigenous hybrids studied in this research were developed from high heat tolerant inbred lines that can set seed even at very higher temperature (≥45°C). Thus, at higher temperatures the indigenous hybrids out-yielded exotic maize hybrids by producing more NGE and having higher HUE. Similar results were also obtained by Yousaf et al. (2018), who concluded that indigenous maize hybrids were more heat-tolerant than exotic hybrids.

Table 6 - Association between different plant traits, temperature indices and grain yield in maize hybrids under Kharif and spring sowing condition.

Variables	Pn	NGE	Protein	DM	PTI	HUE	GDD	GY
Pn		0.304	0.485	0.455	-0.638	0.826	0.328	0.854
NGE	0.408		-0.277	0.184	0.132	0.618	0.244	0.624
Protein	0.415	0.687		0.025	-0.725	0.308	-0.173	0.271
DM	-0.226	-0.348	-0.576		-0.489	0.218	0.971	0.404
PTI	0.287	0.402	0.616	-0.995		-0.233	-0.265	-0.290
HUE	0.691	-0.121	0.174	-0.071	0.091		0.180	0.980
GDD	-0.171	-0.298	-0.532	0.996	-0.983	-0.050		0.369
GY	0.675	-0.146	0.130	0.017	0.005	0.996	0.038	

* (GY= Grain yield per hectare ($Kgha^{-1}$), Pn= Photosynthetic rate ($\mu molm\text{-}2s^{-1}$), NGE= Number of grains per ear, Protein = Grain Protein Percentage (%), DM= Days to maturity, CHU= Cumulative heat units, HUE= Heat use efficiency, PTI= Photothermal index)

* Upper diagonal values represent the association under spring season while lower diagonal values represent the association under Kharif season

* Values represented in bold are significantly different from rest of the values (at 0.05)

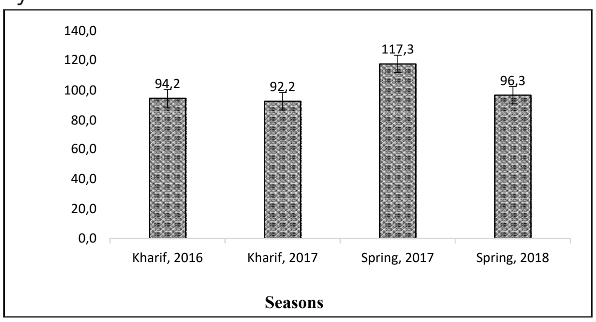

Fig. 4 - Seasonal efficiency of maize hybrids.

Correlation analysis

Correlation analysis revealed significant associations among plant traits in both seasons (Table 6). Grain yield had a highly significant positive correlation with net photosynthetic rate (0.675**) and HUE (0.996**) in kharif seasons. Similarly, in spring seasons, grain yield had a significant positive relationship with net photosynthetic rate (0.854**), NGE (0.624**) and HUE (0.996**). A very weak but positive association was observed between grain yield and CHU (0.038^{NS}) during kharif seasons. In contrast, a comparatively stronger positive but nonsignificant association was observed between grain yield and CHU (0.369^{NS}) in spring seasons (Table 6). As grain yield is a complex, quantitative trait, so direct selection for grain yield is not a suitable criterion. The better option is to select for yield-related traits that are positively associated with grain yield. In this study, grain yield was found to be highly correlated with net photosynthetic rate, number of grains per ear and heat use efficiency under kharif and spring seasons. Similar results were also reported by many researchers who showed the presences of significantly positive correlation of grain yield with number of grains per ear, net photosynthetic rate and heat use efficiency (Thavaprakaash et al. 2007; Inamullah, 2011; Sun et al., 2018).

Seasonal efficiency

Estimating seasonal efficiency is important to determine the suitability of a crop for a specific season. In the current study, seasonal efficiency was calculated for each of the four seasons studied here; the results are presented in Fig. 4. The highest seasonal efficiency was observed in spring 2017 (117.3%) followed by spring 2018 (96.3%) and kharif 2016 (94.2%). The lowest seasonal efficiency was seen in kharif 2017 (92.2%). Overall, seasonal efficiency in spring seasons was 14.59% higher than in kharif seasons, due to higher mean yields (Fig. 4). Those seasons with a seasonal efficiency of 100% or higher are generally considered suitable for crop cultivation. The present results suggest that spring is the best season for maize cultivation, given that its seasonal efficiency was 14% greater than the kharif season as observed by Thavaprakaash et al. (2007) that maize growing seasons differed significantly for their efficiency regarding grain yield mainly due to the variations in ambient temperature.

Conclusions

The maize hybrids investigated in this study differed significantly in plant traits when sown in different growing seasons. Net photosynthetic rate, number of grains per ear and heat use efficiency were found to be the most important traits for improving grain yield in spring-sown maize hybrids. However, net photosynthetic rate and heat use efficiency were the plant traits that contributed to higher grain yields in kharif-sown hybrids. Among different temperature indices, cumulative heat units and heat use efficiency better explained the variations in grain yield across two contrasting environments (spring and kharif) and could be used as selection criteria for the development of high-yielding, heat-tolerant maize hybrids. The present results also indicated that indigenous maize hybrids produced higher yields and were more heat tolerant than exotic hybrids due to the high adaptability and heat tolerance capacity of their parental inbred lines (can set seed above 44 °C) that were developed under local, extreme temperature conditions over the years. An analysis of seasonal efficiency showed that the spring season was more suitable for the cultivation of maize crops than the kharif season.

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