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Seasonal differences in growth, photosynthetic pigments and gas exchange properties in two greenhouse grown maize (*Zea mays* L.) cultivars

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Abstract – The greenhouse (GH) effect has emerged as a major factor in changing cropping patterns and limiting crop yields. This study was conducted to determine the comparative growth and photosynthetic responses of selected heat-resistant (cv. Sadaf) and heat-susceptible (cv. Agatti-2002) cultivars of maize to simulated GH conditions during spring and autumn seasons at seedling, silking and grain filling stages in 2007. Fifteen day old plants were shifted to plexiglass-fitted canopies to create GH conditions and data were recorded at each growth stage. The results revealed that the seasons, GH conditions and cultivars had large effects on plant growth and photosynthetic attributes. Simulated GH conditions increased the canopy temperature 4–7 °C in spring and 3–5 °C in autumn, but increased relative humidity by 2–3% in spring and 5–9% in autumn season. Although GH reduced the growth of both cultivars, shoot dry mass was reduced more in spring grown heat-susceptible maize at all growth stages. Although the cultivars showed a decrease in growth and photosynthesis, GH conditions resulted in less damage to cv. Sadaf than cv. Agatti-2002 in both seasons. Major indicators of sensitivity to GH effect were loss of chlorophyll *b* and carotenoids, reductions in net photosynthesis and stomatal conductance, and possibly reduced ability of Rubisco to fix CO_2 in sensitive maize.

Keywords: canopy temperature, gas exchange, greenhouse effect, growth, maize, photosynthesis

Abbreviations: Car – carotenoid, C_i – leaf substomatal CO_2 concentration, Chl-*a* – chlorophyll *a*, Chl-*b* – chlorophyll *b*, Chls – total chlorophylls, E – leaf transpiration rate, GH – greenhouse, g_s – stomatal conductance, PAR – photosynthetically active radiations, P_n – net photosynthesis

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Introduction

The greenhouse (GH) effect on plants arising from the increased concentration of greenhouse gases and resulting in increased ambient temperature has emerged as a major growth-limiting factor for most crop plants. The GH effect results in increased canopy temperature that causes reduction of plant biomass (Blum 1988, Hussain et al. 2010). Heat stress directly alters photosynthetic acclimation and physiological processes and indirectly changes the pattern of development (Mahmood et al. 2012, Arbona et al. 2013). In different studies, high temperature caused a decrease in growth, transpiration, respiration and photosynthesis and final economic yield (Karim et al. 2000, Stone 2001).

Optimal photosynthesis has a fundamental importance for the carbon accumulation, growth and biomass production of different plant species. Sub-optimal growth conditions affect all the aspects of photosynthesis. High temperature significantly inhibits net photosynthesis (P_n) and stomatal conductance (g_s) in many plant species (Crafts-Brandner and Salvucci 2002, Morales et al. 2003). The P_n in developed and nearly developed leaves was more sensitive than in developing leaves (Karim et al. 1999). Photosynthetic apparatus is highly sensitive to high temperature and inhibited when the leaf temperature exceed 38 °C (Crafts-Brandner and Salvucci 2002). High temperature reduces the activation state of Rubisco, which is the most susceptible component of the photosynthetic apparatus in both C_3 and C_4 plants (Crafts-Brandner and Salvucci 2002, Salvucci and Crafts-Brandner 2004, Luo et al. 2011). Extensive studies have shown that both photosystems are damaged by increasing temperature during photosynthesis, thus leading to reduced photosynthetic efficiency (Szilvia et al. 2005, Du et al. 2011).

Maize (*Zea mays* L.) is a C_4 plant and has a distinctive leaf anatomy and photosynthetic metabolism (Taiz and Zeiger 2010). Both photosynthesis and growth of C_4 plants respond positively towards elevated ambient CO_2 (Ghannoum et al. 2000). The rate of leaf development and P_n in maize is at maximum near 31 to 34 °C (Tollenaar 1989, Yan and Hunt 1999, Kim et al. 2007) at ambient CO_2, but decreased at temperatures above 37 °C while complete inhibition occurred near 45 °C (Crafts-Brandner and Salvucci 2002). However, there are great intraspecific differences in maize for tolerance to ambient environmental changes.

In the era of climate change, the GH effect has attained major importance and thus led scientists to study precisely its influence on the photosynthetic properties of important crop species. To adapt to changes in the environment, plants have evolved a number of physiological and biochemical strategies. Leaf photosynthesis plays an important role in the adaptation of plants to changing environmental conditions, but this also depends upon the type of species and the growth stage. Limited reports have highlighted the specific growth and photosynthetic responses of plants to current and upcoming changes in the climatic conditions. The present study was undertaken to determine the changes in growth, pigment composition and gas exchange attributes of selected differentially heat-responsive maize cultivars grown in GH conditions.

Materials and methods

Source of maize seed, treatment and plant growth conditions

Seeds of selected maize (*Zea mays* L.) cultivars Sadaf (heat-tolerant) and Agatti-2002 (heat-sensitive) were obtained from the Maize and Millets Research Institute (MMRI), Yousafwala, Sahiwal, Pakistan. The experiments were conducted in the wire-house of the Department of Botany, University of Agriculture, Faisalabad, Pakistan during the spring and autumn seasons of 2007. Seeds of both cultivars were grown in plastic pots, 30 cm high, 82 cm in circumference at the top and 70 cm at the bottom. A hole was made in the bottom for leaching during replacement of the soil solution. Each pot contained 13 kg of dry sand, which was washed thoroughly with tap water followed by distilled water before filling in the pots. Ten seeds of both cultivars were sown. After germination, the pots were given half strength nutrient solution (HOAGLAND and ARNON 1950) after four days in an amount to drain the previous solution. Five healthy and equal sized, three-day old seedlings were retained in each pot for making determinations at seedling, silking and grain filling stages. Greenhouse conditions were created by shifting the pots containing growing plants to the canopies that were placed in a wire-house at the above growth stages, whilst the control set was kept outside the canopies in a wire-house. The top of the wire- house was covered with polythene sheeting to produce the light transmission index of 75 to 80% in and outside the canopy. Moreover, by measuring PAR using an open system portable infrared gas analyzer (IRGA; LCA-4, Analytical Development Company, Hoddesdon, England), it was noticed that the plants inside and outside the canopy had PAR (400–700 nm) at the leaf surface in the range 1185–1204 μmol m^{-2} s^{-1} between 10 and 11 am. The temperatures and relative humidity inside and outside the canopies were recorded in both the seasons just above the plant height (Fig. 1). The plants were kept inside the canopies for 20 days at each of the growth stages, and harvesting was done after 15 days of treatment application.

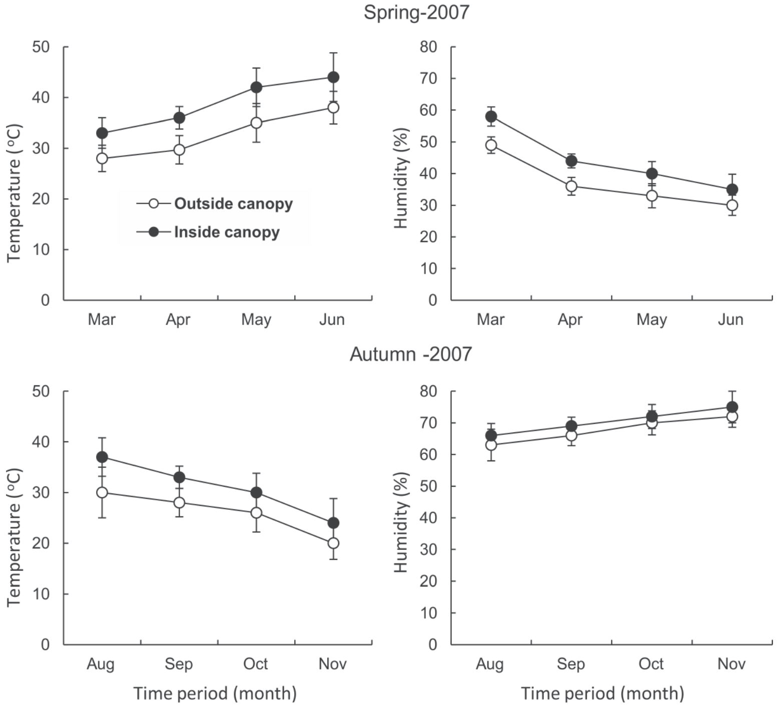

Fig. 1. Variation in the temperature and relative humidity inside and outside the plexiglass fitted canopy during an experiment in spring and autumn seasons in 2007.

For the determination of Chl-*a*, Chl-*b*, their total and total carotenoid (Car) contents, the third leaf (0.5 g) from the top was excised and homogenized with pestle and mortar in 80% acetone; volume was made up to 5 mL and filtered. The absorbance was measured at 480 nm for Car, and at 645 and 663 nm for Chl-*a* and Chl-*b,* respectively, using a spectrophotometer (Hitachi-U-2001, Japan). Chl-*a,* Chl-*b*, their total content and their Chl-*a:*Chl-*b* ratio were calculated as described by YOSHIDA et al. (1976), while Car were computed with the formula of DAVIES (1976).

Gas exchange characteristics were measured by IRGA of the third leaf (from the top) of each plant. Measurements were performed from 10:00 am to 11:00 am with the following leaf chamber adjustments: leaf surface area 11.35 cm^2, ambient CO_2 concentration 357 $\mu mol\ mol^{-1}$, temperature of leaf chamber varied from 32.5 to 37 °C, leaf chamber gas flow rate 392.8 $ml\ min^{-1}$, molar flow of air per unit leaf area 440 $\mu mol\ m^{-2}\ s^{-1}$, ambient pressure 99.6 kPa, water vapor pressure in to chamber ranged from 20.5 to 23.1 mbar, PAR (Q leaf) on leaf surface ranged from 975 to 1250 $\mu mol\ m^{-2}\ s^{-1}$.

Statistical analysis

The experimental design was completely randomized with four replications per treatment. The presence or absence of significant differences between different factors at P = 0.05 was ascertained with analysis of variance (ANOVA). The means were compared to find significant differences among them using least significant difference. Computer software COSTAT (CoHort software, 2003, Monterey, California, USA) was used for all statistical analysis and MS-Excel was used to graphically present the data.

Results

Plant dry mass

Data for changes in shoot dry weight indicated significant ($P < 0.01$) difference in cultivars and growth stages during spring but not during autumn. However, for root dry weight, such an interaction was notable at silking and grain filling stages in spring only (Tab. 1). Shoot dry weight during spring was reduced at seedling stage in both cultivars, although cv. Sadaf indicated a lower reduction (10%) than cv. Agatti-2002 (39%) in GH conditions. At silking stage, cv. Sadaf showed an increase (5%) and cv. Agatti-2002 a decrease (36%) in shoot dry weight. At grain filling stage, shoot dry weight was reduced in both cultivars, but this reduction was lower (3%) in cv. Sadaf than in cv. Agatti-2002 (30%). In autumn, although the trend of changes in shoot dry weight was similar to that observed during spring, except at the grain filling stage when cv. Sadaf indicated an increase while cv. Agatti-2002 showed a decrease in shoot dry weight under GH conditions. Root dry weight declined in both cultivars although the reduction was less (~18%) in cv. Sadaf than in cv. Agatti-2002 (~26%) during spring at the seedling stage. At silking and grain filling stages, cv. Sadaf showed an increase (~8 and 5%, respectively) and cv. Agatti-2002 a decrease (34 and 32%, respectively) in root dry weight. In autumn, there was a reduction of root dry weight in both cultivars but cv. Agatti-2002 suffered more than cv. Sadaf (~22 and 6%, respectively). At silking and grain filling stages, cv. Sadaf showed an increase (~41 and 4%, respectively) but cv. Agatti-2002 a decrease (~20 and 34%, respectively) in root dry weight.

Tab. 1. Effect of greenhouse conditions on dry weight of maize plants grown during spring and autumn in 2007. The comparisons have been made of the cultivars separately for seasons and growth stages. The values sharing same letter differ non-significantly (P > 0.05).

Seasons	Growth stages	Cultivars	Shoot dry weight (g)		Root dry weight (g)	
			Control	Greenhouse	Control	Greenhouse
Spring	Seedling	Sadaf	3.82^{a}	3.43^{b}	1.65^{a}	1.36^{a}
		Agatti-2002	3.02^{c}	1.84^{d}	1.89^{a}	1.40^{a}
	Silking	Sadaf	17.52^{a}	18.44^{a}	3.82^{a}	4.12^{a}
		Agatti-2002	15.85^{ab}	10.12^{c}	3.27^{b}	2.16^{c}
	Grain filling	Sadaf	60.93^{a}	58.89^{ab}	11.67^{abc}	12.24^{ab}
		Agatti-2002	49.52^{bc}	34.64^{d}	11.86^{abc}	8.06^{c}
Autumn	Seedling	Sadaf	4.90^{a}	4.09^{a}	1.80^{a}	1.69^{a}
		Agatti-2002	3.18^{a}	3.03^{a}	1.84^{a}	1.44^{a}
	Silking	Sadaf	13.84^{b}	15.52^{ab}	3.24^{a}	4.57^{a}
		Agatti-2002	13.05^{bc}	12.83^{bc}	2.88^{a}	2.63^{a}
	Grain filling	Sadaf	50.02^{b}	51.40^{ab}	12.90^{ab}	13.44^{a}
		Agatti-2002	55.90^{a}	39.50^{cd}	13.78^{a}	9.16^{bc}

Photosynthetic pigments

The GH conditions differentially modulated the contents of photosynthetic pigments in both maize cultivars. In the case of Chl-*a*, no significant (P > 0.05) interaction of cultivars and growth conditions under the GH effect was noted at seedling stage in the spring season, at silking stage in both seasons and grain filling stage during autumn. The seedling stage data showed that cv. Sadaf showed no significant differences in both seasons, whilst cv. Agatti-2002 indicated a decline of ~7 and 21%, respectively in both of the seasons in GH conditions. At silking stage, Chl-*a* was not changed in cv. Sadaf but decreased (~18%) in cv. Agatti-2002 during spring while it increased by 7 and 11% in both cv. Sadaf and cv. Agatti-2002 in autumn, respectively. At grain filling stage in spring, cv. Sadaf exhibited an increase (4%) but cv. Agatti-2002 a decrease (~14%) of Chl-*a*. However, the responses of the two cultivars were similar in autumn in GH conditions (Fig. 2).

Data for changes in Chl-*b* indicated no significant interaction (P > 0.05) of cultivars and growth conditions at any growth stages under the GH effect. Data recorded at seedling stage indicated an increased Chl-*b* by cv. Sadaf (~4%) during spring and autumn seasons, but cv. Agatti-2002 showed a decreased Chl-*b* during spring (10%) but no change during autumn. At silking stage, Chl-*b* increased in cv. Sadaf during spring (~7%) but declined in autumn (~13%), whilst in cv. Agatti-2002 it declined in both seasons (~16 and 47% in spring and autumn, respectively). At grain filling stage, Chl-*b* was reduced less in cv. Sadaf (~11%) than in cv. Agatti-2002 (~21%) during spring. In autumn, Chl-*b* increased in cv. Sadaf (~14%) but did not change in cv. Agatti-2002 in GH conditions (Fig. 2).

Data for leaf total Chls content showed no significant (P > 0.05) interaction of seasons and cultivars under prevailing GH conditions at any growth stage except during the spring at grain filling stage, when there was a significant (P < 0.01) interaction for cv. Agatti-2002

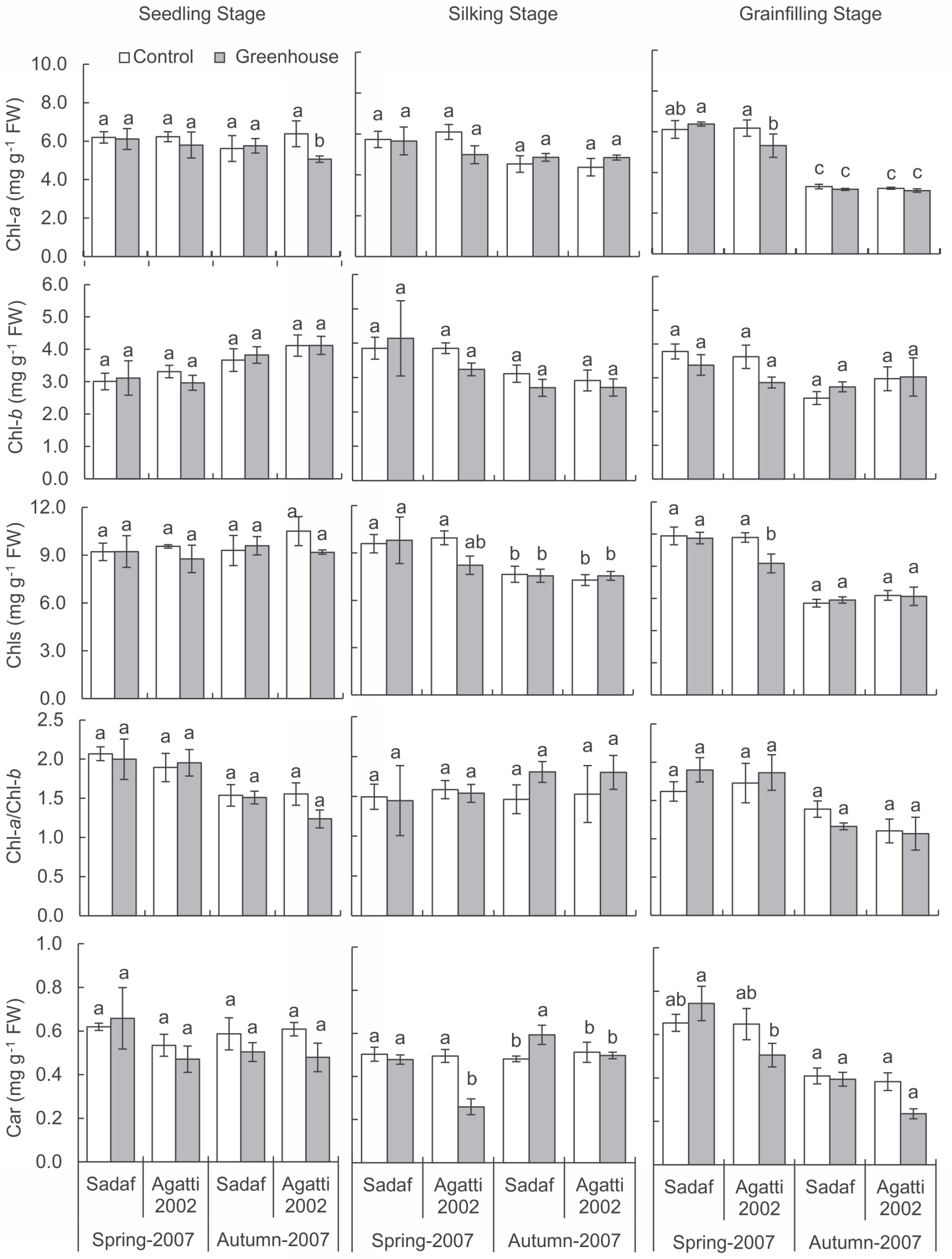

Fig. 2. Changes in photosynthetic pigments in the control and greenhouse grown plants of maize cultivars during spring and autumn seasons at three growth stages. The comparisons have been made of the cultivars separately for spring and autumn seasons, the data bars carrying same letter in a season differ non-significantly ($P > 0.05$); FW – fresh weight.

cultivar. At seedling, silking and grain filling stages, cv. Sadaf showed similar amounts of total Chls in spring and autumn seasons, while cv. Agatti-2002 indicated a marked reduction in total Chls in autumn at seedling stage (~13%) and in spring at silking (~17%) and grain filling (~16%) stages under the GH effect (Fig. 2).

For Chl-*a*/Chl-*b* ratio, the interaction of cultivars and GH conditions were non-significant ($P > 0.05$) at both seasons and all the growth stages. At seedling stage, cv. Sadaf revealed a significant reduction in the Chl-*a*/Chl-*b* ratio during both seasons, while cv. Agatti-2002 exhibited an increased Chl-*a*/Chl-*b* ratio (~3%) in spring and declined (~21%) in autumn under GH effect. At silking stage, there was an insignificant reduction (~3%) in Chl-*a*/Chl-*b* in cv. Sadaf during spring, but an increase (~23%) during the autumn, while Agatti-2002 showed an insignificant reduction (~3%) in Chl-*a*/Chl-*b* ratio in spring and increased (~18%) during autumn under GH effect. At grain filling stage, cv. Sadaf showed an increased (~17%) Chl-*a*/Chl-*b* ratio during spring, but a reduction (~16%) during autumn, while in cv. Agatti-2002, this ratio was insignificantly increased (~8%) in spring and declined (~3%) during autumn.

Leaf Car content was affected significantly in cv. Agatti-2002 at silking stage during spring due to the GH effect. The interaction of cultivars and GH conditions was not significant ($P > 0.05$) at seedling stage during either season, it was significant ($P < 0.01$) during both seasons at silking stage, while at the grain filling stage the cultivars and GH condition interactions were significant during spring and non-significant ($P > 0.05$) during autumn. At seedling stage, cv. Sadaf indicated an increase (~6%) of the Car during spring, but a reduction (~14%) during the autumn season, while cv. Agatti-2002 indicated a reduction of ~12% during spring and of ~21% in autumn under GH effect. At silking stage there was an insignificant reduction (~5%) in Car in cv. Sadaf during spring, but an increase (~23%) during autumn, while cv. Agatti-2002 showed a marked reduction (~48%) in Car in spring and an insignificant reduction (~3%) during autumn under GH effect. At grain filling stage, cv. Sadaf again exhibited an increase (~14%) of Car during spring but an insignificant reduction (~4%) during the autumn season, while in Agatti-2002 a marked reduction was noted during spring (~22%) and autumn (~39%) (Fig. 2).

Gas exchange parameters

Leaf P_n was significantly affected due to the GH effect and the response of cultivars was different at different growth stages attained in both the seasons. For this attribute, the interaction of cultivars and GH conditions were significant ($P < 0.05$) at seedling stage in both seasons. At the seedling stage in the spring season, leaf P_n decreased by ~28% in cv. Sadaf and showed a marked decline (~37%) in cv. Agatti-2002, while in autumn season there was a nominal reduction (~ 4%) in cv. Sadaf and a marked reduction (~21%) in cv. Agatti-2002. At silking and grain filling stages, although both the cultivars showed a reduction in P_n, a particularly significant reduction (~60% and ~57%) was noted in cv. Agatti-2002 under the GH effect in both seasons (Fig. 3).

For leaf transpiration rate (E), the interactions of cultivars and GH conditions were non-significant ($P > 0.05$) at both of seasons and growth stages (seedling and silking) except for a significant ($P < 0.05$) interaction of cultivars and GH conditions at grain filling stage. GH conditions did not have effect in spring-grown plants in any of the maize cultivars at seedling stage (Fig. 3). At silking stage in the spring, no specific reduction in E in any of the

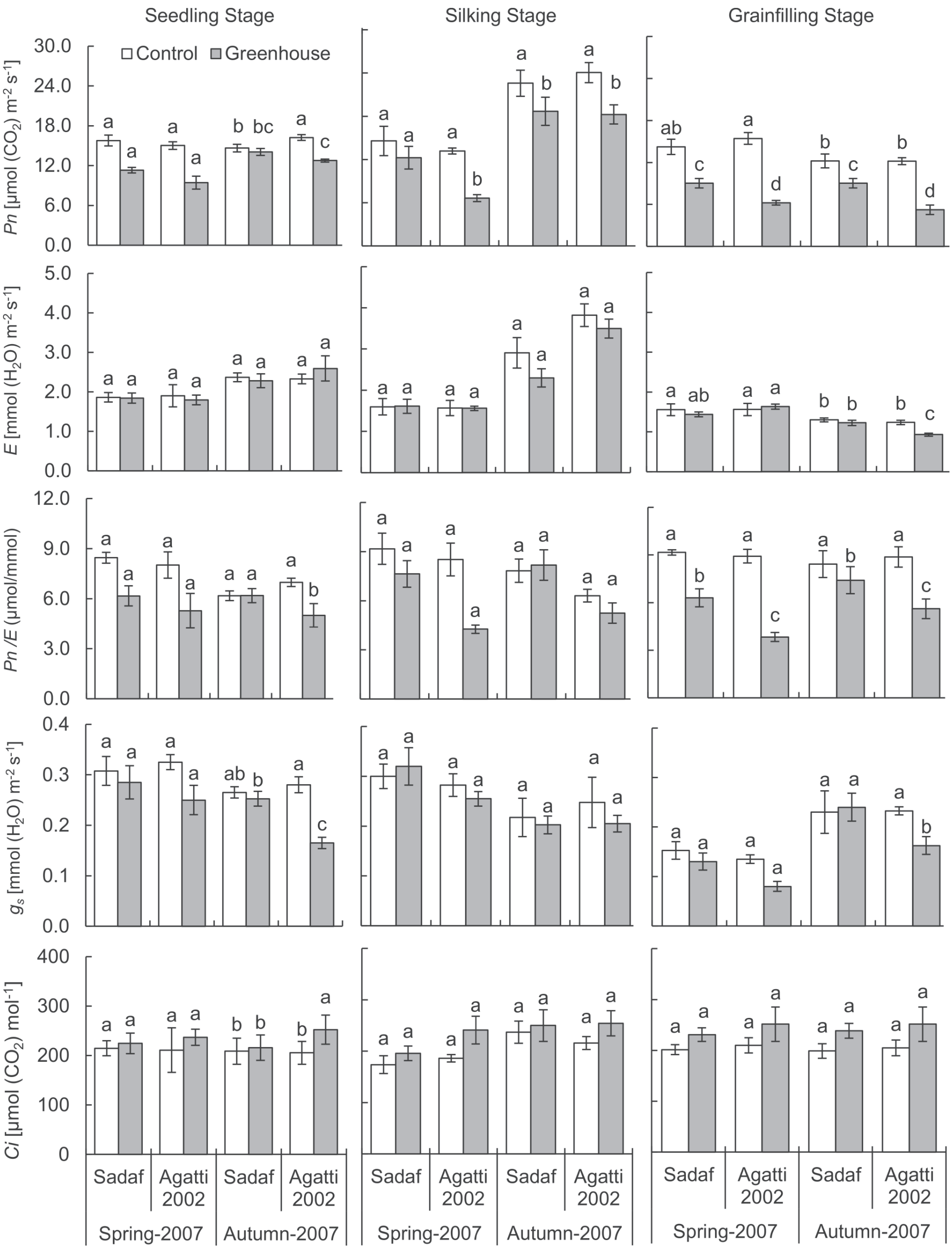

Fig. 3. Changes in gas exchange parameters of the control and greenhouse grown plants of maize cultivars during spring and autumn at three growth stages. The comparisons have been made of the cultivars separately for spring and autumn, the data bars carrying same letter in a season differ non-significantly ($P > 0.05$).

cultivars was recorded, while in autumn, a greater reduction (~20%) was evident in cv. Sadaf and a lesser one (~9%) in cv. Agatti-2002 in GH conditions. At the grain filling stage E was the same as for silking stage in the spring for both cultivars and just slightly less than in the seedling stage. Only in autumn was E reduced (~25%) in cv. Agatti-2002 from the previously mentioned stages (Fig. 3).

In leaf water use efficiency, measured as P_n/E, a significant interaction of cultivars and GH conditions was evident during the autumn at seedling stage ($P < 0.05$) and at silking ($P < 0.01$) and grain filling ($P < 0.01$) stages during both seasons. A greater reduction at seedling (~34%) and silking stage (~50%) was recorded in P_n/E due to GH effect in cv. Agatti-2002 than in cv. Sadaf in the spring. However, in the autumn, P_n/E was not affected in cv. Sadaf, but markedly reduced at seedling (~28%) and silking (~17%) stage in cv. Agatti-2002. At grain filling stage, this reduction in P_n/E was recorded in both maize cultivars in both the seasons, being much greater (~57%) during spring and (~43%) in autumn in cv. Agatti-2002 under the GH effect (Fig. 3).

The interaction of cultivars and GH conditions for leaf stomatal conductance (g_s) was non-significant ($P > 0.05$) for both seasons and all growth stages except during the autumn for seedlings and both seasons for the grain filling stage, which exhibited a significant ($P < 0.05$) interaction of these factors. At the seedling stage g_s was reduced slightly (~7%) in cv. Sadaf and greatly (23%) in cv. Agatti-2002 during spring, while in autumn there was no great reduction in this attribute in cv. Sadaf although there was a marked reduction (41%) in cv. Agatti-2002 in the GH. At the silking stage in the spring season, the g_s increased (7%) in cv. Sadaf but declined (~10%) in cv. Agatti-2002, while in the autumn season, both cultivars indicated declines in this attribute. At grain filling stage, GH conditions produced a little decline in the g_s of cv. Sadaf (~14%) while cv. Agatti-2002 was more affected (~41%) in the spring, while in autumn the g_s was not affected in cv. Sadaf but markedly declined (30%) in cv. Agatti-2002 in the GH conditions (Fig. 3).

The interaction of cultivars and GH conditions for leaf substomatal CO_2 concentration (C_i) was non-significant ($P > 0.05$) for both seasons and all growth stages except during the autumn at seedling stage, when a significant ($P < 0.05$) interaction of these factors was observed. Leaf C_i was increased in both cultivars at all growth stages due to GH effect but cv. Sadaf indicated a lower value of this parameter than cv. Agatti-2002. The C_i increased greatly in cv. Agatti-2002 in autumn at seedling stage (23%), during the spring at silking stage (29%) and during the autumn at grain filling stage (23%), while in cv. Sadaf it increased slightly at all these stages (Fig. 3).

Discussion

Significant interactions of the cultivars and treatments for different attributes appeared in one season and disappeared in another season at different phenological stages (Figs. 2 and 3; Tab. 1). This showed that the prevailing GH conditions produced a lot of changes in maize growth pattern as well as in the photosynthetic system, even though the effects were less in the heat tolerant (cv. Sadaf) than the sensitive cultivar (cv. Agatti-2002). In such conditions, plants undergo a depression in visual growth and development, but the extent of reduction depends greatly upon the type of stress, its severity and duration (Ahmed et al. 2012, Arbona et al. 2013, Galani et al. 2013). Greater dry weight results from the extent of the available photosynthetic area together with an enhanced capacity of leaves to photosynthesize (Karim et al. 2000, Huve et al. 2006, Suarez and Medina 2006).

The results of this experiment revealed that both of maize cultivars indicated quite a lot of changes in Chl-*a*, Chl-*b*, total Chls, Chl-*a*/Chl-*b* ratio and Car contents in both growing seasons and all growth stages (Fig. 2). Of two chlorophyll species, Chl-*b* was more damaged than Chl-*a* by prevailing GH high temperature condition (Fig. 2), leading to an overall loss of chlorophylls (Fig. 2), thereby causing more yellowing of leaves in cv. Agatti-2002 than in cv. Sadaf. These changes resulted in an increased Chl-*a*/Chl-*b* ratio (Fig. 2), which was slightly higher in spring at the seedling stage. It has been shown that high temperature enhances chlorophyllase activity, which degrades the chlorophylls and reduces their contents (Todorov et al. 2003, Wahid et al. 2007). Of the two chlorophyll species, Chl-*b* is more prone to degradation by heat stress, especially during the spring when the temperature is sufficiently high and leaf nitrogen contents (not reported here) might have been reduced (Matile and Hörtensteiner 1999). From these changes in the chlorophyll concentrations, it can be deduced that the sensitivity of Chl-*b* to GH condition is mainly responsible for the yellowing of leaves, particularly in spring grown plant. From the prevailing temperature conditions in the canopy grown plants in spring compared to autumn, it can be seen that plants sown in spring months had to face more adverse temperatures at later growth stages (silking and grain filling), than the autumn grown plants, which do not experience such a high temperature and greater relative humidity during these growth stages (Hussain et al. 2010). Thus, it can be inferred that GH conditions are more detrimental to the photosynthetic machinery of the spring sown plants in the warmer months.

Carotenoids have dual roles in plants. By acting as accessory light harvesting pigments, they harvest the light and funnel it onto the photosystem. The other important role of carotenoids remains the alleviation of oxidative damage to the biological membranes via the xanthophyll cycle (Havaux 1998). Environmental stress to the tolerant plants is reported to increase Car contents as compared to control counterparts, which suggests they have a role in the stress tolerance (Wahid 2007, Arbona et al. 2013). In the present research, it was noted that tolerant maize (cv. Sadaf) in the GH conditions either showed increased, steady state or minimal decrease in Car contents during both the seasons as compared to sensitive maize (cv. Agatti-2002), which displayed decreased Car content in both the seasons. However, these decreases were more remarkable in the spring- than in the autumn-grown maize plants (Fig. 2). Thus, in concurrence with previous reports (Wahid et al. 2007), these data substantiated a crucial and profound role of carotenoids in the relatively adverse condition like GH, where increased temperature and changes in GH are the main determinants of growth.

Plant productivity is assessed on the basis of efficiency of a plant to fix CO_2 and production of photo assimilates by the leaves (source tissue) for export to various sinks for utilization and storage (Rajcan and Tollenaar 1999, Luo et al. 2011). Maize, like a number of other crop plants, also shows great changes in CO_2 fixation under suboptimal growth conditions (Tollenaar 1989, Sinsawat et al. 2004). In this study, the leaf gas exchange data revealed that the growing season and GH conditions had a great influence on these attributes of both the cultivars. Leaf P_n, E and g_s were little affected at seedling, reduced more at silking and reduced the most at grain filling stage under GH conditions, while Agatti-2002 showed greater sensitivity to GH conditions during all the stages (Fig. 3). The P_n/E increased more in spring-grown maize than in autumn-grown maize (Fig. 3), whilst Ci indicated a greater decrease in spring than in autumn (Fig. 3). The data suggested that such declines in CO_2 fixation by the sensitive maize was mainly due to reduced g_s and reduced activity of Rubisco in absorbing CO_2 and reduction of assimilate production via the Calvin cycle in the mesophyll cells (Douthe et al. 2011).

As mentioned above, both photosynthetic pigments and gas exchange parameters are the fundamental processes involved in dry matter yield. Therefore, optimal operation of reactions in both these processes is important. Studies highlighting the proportionate changes in these processes are scanty. In the present study, we noted that the pattern of changes in Chl-*b* was similar to the patterns of g_s and C_i, which indicated that prevailing seasonal conditions were equally deterrent to all these attributes. Despite the fact that the photosynthetic pigment and gas exchange parameters are entirely different in nature and composition, these results show that parallel changes in both are important determinants of maize growth.

In conclusion, changes in the canopy temperature and relative humidity due to GH conditions were responsible for alteration in plant dry masses and photosynthetic attributes in maize, across spring and autumn season, although the latter was less adverse. The results have great implications in the production of such crop cultivars, which may be well adapted to upcoming changes due to GH effect.

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