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Study of physiological responses of *Allium sativum* to elevated CO_2 and temperature

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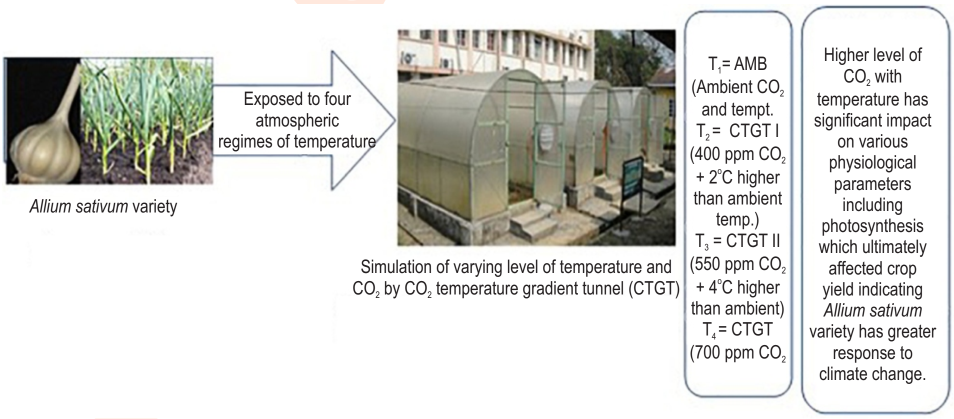
Abstract

Aim: The present investigation was undertaken to study the response of some garlic varieties of *Allium sativum* under different ambient and elevated CO_2 and temperature conditions in order to investigate the physiological responses under changing climatic condition.

Methodology: A two factorial CRD experiment was conducted for two years with four varieties of *Allium sativum* (Ekfutia Assam, Assam Local, Bhima Omkar and Bhima Purple) under four atmospheric regimes [T_1= Ambient CO_2 and temperature; T_2= Carbon dioxide Temperature Gradient Tunnel-I (400 ppm CO_2 + 2°C higher than ambient); T_3 = Carbon dioxide Temperature Gradient Tunnel-II (550 ppm CO_2 + 4°C higher than ambient); T_4 = Carbon dioxide Temperature Gradient Tunnel-III (700 ppm CO_2 + 6°C higher than ambient)]. Major changes in physiological parameters of the varieties were recorded in Carbon dioxide Temperature Gradient Tunnel-II as compared to ambient condition. The rate of photosynthesis was measured on fully expanded youngest leaves of each sample plant using a portable Infrared Gas Analyzer.



Results: The mean photosynthetic rate of all four varieties grown over two years was 13.43% higher in Carbon dioxide Temperature Gradient Tunnel-II over varieties grown for two consecutive years under Ambient CO_2 and temperature. However, high CO_2 concentration and temperature stress significantly reduced the stomatal conductance approximately by 27.48%.

Interpretation: The results of this study gives a comprehensive analysis of garlic varieties under four different climatic conditions of CO_2 and temperature and revealed that Ekfutia Assam and Assam Local and garlic varieties Bhima Omkar and Bhima Purple were promising varieties as they responded significantly to elevated CO_2 and temperature regimes. This may provide some critical inputs for optimizing the strategies in future farming and farming opportunities of this commercially and medicinally important crop under changing climatic conditions.

Key words: Carbon-di-oxide, Garlic varieties, Photosynthesis, Stomatal conductance, Temperature

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Introduction

There is an increasing trend in the atmospheric CO_2 concentration since 1950 due to the anthropogenic activities of human creating a major concern on the global climate change (More *et al.,* 2017). The CO_2 concentration in atmosphere steadily increased from 316 ppm in 1959 which is expected to double by the end of 21st century (IPCC, 2001 and IPCC, 2007). This has drastically altered the carbon footprint in the biosphere by interrupting the photosynthetic carbon assimilation in plants (Bazzaz, 1990; Houghton *et al.,* 1990; Jobe *et al.,* 2020). The photosynthetic efficiency doubles when plants are exposed to a higher concentration of CO_2, *viz.,* 700 ppm as compared to 380 ppm as elevated CO_2 increases the net photosynthesis rate and biomass accumulation in C_3 plants (Cruz *et al.,* 2014). These positive effects of increased CO_2 on plant growth under increased temperatures have resulted in enhancement of photosynthetic rate with reduction in stomatal conductance (Kirkham, 2011; Yu, *et al.,* 2012). Many studies have highlighted the biological responses to CO_2 enrichment (Ainsworth and Rogers, 2007; Kim *et al*., 2013).

Elevated CO_2 decreases stomatal conductance and limits the CO_2 fixation rate but promotes water use efficiency and photosynthetic rate and, consequently increases plant growth and production (Ainsworth and Rogers, 2007; Xu *et al.,* 2016). A significant increase in yield of vegetables like potato at 1000 ppm CO_2 and root yield of sweet potato at 750 ppm CO_2 were observed by various workers like Wheeler *et al*., (1994); Mortley *et. al*., (1996); Ainsworth and Long, (2005); Singh and Jasrai (2012) and Zhang *et al*., (2015). The photosynthetic rate of sweet potato increased under controlled conditions due to increase in CO_2 from 250 to 560 ppm. There was also a significant increase by 31 – 43% in above and 61 – 101% in below ground biomass of sweet potato at 1520 ppm of CO_2. It implies that there is greater accumulation of below ground biomass in comparison to the above ground biomass under elevated CO_2 regime (Cen and Sage, 2005; Xu *et al.,* 2016). Garlic (*Allium sativum* L.), considered as "Nectar of life in Ayurveda", is both a commercially and culturally important crop worldwide as it contains more than 100 biologically useful chemicals which lowers cholesterol, fights off viruses and thus help in development of immunity (Richard, 2001).

It is a world famous spice commonly used for its medicinal properties. During 2017-18, the production of garlic in India was 17.21 lakh tonnes from 3.03 lakh ha area (NHRDF, 2018) which has increased to 29.16 lakh tonnes from 3.62 lakh ha area (Annon, 2020). Although India is the second largest garlic producer after China in the world, its productivity is still very low, *i.e.,* 5.68 tonnes ha^{-1} in 2017-18, as compared to 16.71 tonnes ha^{-1} of world average. Thus, there is a demand to increase the productivity to 6.77 tonnes ha^{-1} against the existing 5.68 tonnes ha^{-1} (NHRDF, 2018). However, India, once an exporter of garlic, is now importing it to meet the domestic requirement. Despite its immense medicinal properties, there have been very few studies on its growth and development under influence of elevated atmospheric CO_2 and temperature. There is a need to analyse how this predicted elevation of atmospheric CO_2 and temperature will affect bulb formation in garlic. The growth period of garlic is centered on cold season (Del Pozo and Gozalez, 2005; Ledesma *et al.,* 1997), but in North-east India low yield has been observed due to short cold period with concomitant increase in temperature during bulb formation.

The life cycle of garlic, particularly from late plantings may be extended to the period when temperature becomes high, and rainfall prevails which exert unfavourable effects on growth and development. A long photoperiod of more than 2 weeks is required for dormancy induction of axillary buds and bulb formation (Mathew *et al.,* 2011). As a result, bulb production is low and in some cases a percentage of the plant does not initiate bulbs at all. This low production leads to wide range of price variation in the market. To achieve this increasing demand is a big challenge with respect to future climatic changes (Fischer *et al.,* 2005). Thus, the present study was conducted to determine the physiological characters of garlic (*Allium sativum* L.) varieties under elevated CO_2 and temperature regimes.

Materials and Methods

The study was carried out under controlled environment of Carbon dioxide temperature gradient tunnel (CTGT), in the Department of Crop Physiology, Assam Agricultural University, Jorhat to investigate the differential response of garlic plant growth and development in increased level of CO_2 and temperature. Four garlic varieties used in this study were Ekfutia Assam and Assam Local commonly cultivated in Assam and two national varieties, *viz.,* Bhima Omkar and Bhima Purple. The experiment was conducted in 2 Factorial (variety and environmental condition) Completely Randomized Design with 4 replications. A Carbon dioxide temperature gradient tunnel was constructed with Mild Steel (MS) pipe and covered with a polycarbonate sheet of more than 85% transparency. The dimensions of the tunnel were 50 m (L) x 2.5 m (W) x 2 m (H). There was an air blowing/ heating facility for discharging different temperature of 1 to 6°C.Three different tunnels were used for three varied combinations of temperatures and CO_2 conditions. A control/monitoring system monitors the temperature and humidity with fixed sensors at 3 min interval.

Three different levels of CO_2 and temperature were maintained throughout the entire crop growth period regularly 9 a.m. to 2 p.m. from planting to maturity stage through Infra-Red Heater regulated by Supervisory Control and Data Acquisition (SCADA) software. The garlic cloves were planted according to the following treatments (T): T_1: Ambient CO_2 (380-390 ppm) and temperature; T_2: Carbon dioxide Temperature Gradient Tunnel-I (CTGT-I) (400 ppm CO_2 + 2°C higher than ambient), T_3: Carbon dioxide Temperature Gradient Tunnel-II (CTGT-II) (550 ppm CO_2

+ 4°C higher than ambient); T_4: Carbon dioxide Temperature Gradient Tunnel-III (CTGT-III) (750 ppm CO_2 + 6°C higher than ambient). Data were recorded at 30 days interval from 10 numbers of randomly selected plants per plot when light intensity was 900-1200µE. Leaf Area Index (LAI) at 90 days after planting (DAP) was recorded using Laser Area Meter (model CI 203) (Evans, 1972). Chlorophyll content of leaf was estimated by non-maceration method using dimethyl sulphoxide (Hiscox and Israelstam, 1979). The photosynthetic rate was recorded on fully expanded youngest leaf of each sample plant using a portable Li-cor LI- 6400 Infrared Gas Analyzer (LI-CO 6400USA). Stomatal conductance was measured by Infrared Gas Analyzer as per Centritto *et al.* (1999). The internal CO_2 concentration was calculated from the measured assimilate rate and stomatal conductance. Relative water content (RWC) was calculated by the formula given by Weatherly and Barrs (1962) and was expressed as percentage. The yield per hectare was computed from plot yield and expressed in tonnes ha^{-1}. All the data recorded during two years of experimentation and laboratory analyses were pooled and subjected to analysis of variance by F test (Panse and Sukhatme, 1967). The critical difference values were calculated at 5 per cent level.

Results and Discussion

The perusal of data showed significant differences for all the parameters under observation during both the years of investigation and the results obtained from pooled data are presented in the Tables 1 and 2. LAI was recorded 13.37% higher in Carbon dioxide Temperature Gradient Tunnel–II as compared toambient condition, whereas it was 23.35% lower in Carbon dioxide Temperature Gradient Tunnel-III as compared to ambient. The interaction effect of treatment and variety showed a significant increase in Leaf area index in Carbon dioxide Temperature Gradient Tunnel-I and Carbon-di-oxide Temperature Gradient Tunnel-II, but significant reduction in LAI was recorded in Carbon dioxide Temperature Gradient Tunnel-IIIin case of all the four varieties (Fig. 1A) whereas the highest increase in LAI (19.07%) over ambient condition was observed in case of Ekfutia Assam, a local genotype from Assam in Carbon dioxide Temperature Gradient Tunnel-II, followed by 15.32% increase in Assam Local. However, the highest reduction in LAI (29.60%) was recorded in variety Bhima Omkar under the treatment Carbon dioxide Temperature Gradient Tunnel-III. Increased leaf area may help to increase the photosynthetic area and give room for other biochemical constituents and thereby increase the photosynthetic rate, which was ascertained under present investigation. CO_2 had a greater effect on dry matter partitioning.

Dry matter partitioning in leaf was significantly enhanced by CO_2 enrichment. Liu *et al.* (2002) reported that elevated CO_2 resulted in larger fresh mass, dry mass, leaf area and leaf thickness in two-year-old needles of Sitka spruce (*Picea sitchensis*). Tree height, basal diameter and biomass production were also increased, regardless of nitrogen supply. Therefore, from the present findings, it can be related that in tolerant varieties

Table 1: Two years pooled data on the effect of CO_2 and temperature on various physiological parameters of garlic (*Allium* spp.)

Treatments	Leaf area index (90 DAP)	Total chlorophyll content (mg g^{-1} f.wt.)	Photosynthetic rate (µmol CO_2 $m^{-2}s^{-1}$)	Stomatal conductance (mmol $m^{-2}s^{-1}$)	RLWC (%)	Internal CO_2 concentration (µmol CO_2 mol^{-1})	Bulb yield (t ha^{-1})
AMB	1.72	1.06	19.14	0.60	64.44	330.74	9.36
CTGT I	1.82	1.04	20.68	0.57	64.67	345.91	9.68
CTGT II	1.95	0.97	21.71	0.53	66.58	270.75	10.40
CTGT III	1.32	0.90	15.52	0.43	55.78	300.58	8.13
S. Ed.	0.03	0.02	0.63	0.01	4.35	2.21	0.06
CD (0.05%)	0.07	0.03	1.34	0.02	9.23	4.69	0.13

Table 2: Two years pooled data on the effect of varieties on various physiological parameters of garlic (*Allium* spp.)

Varieties	Leaf area index (90 DAP)	Total chlorophyll content (mg g^{-1} f.wt.)	Photosynthetic rate (µmol CO_2 $m^{-2}s^{-1}$)	Stomatal conductance (mmol $m^{-2}s^{-1}$)	RLWC (%)	Internal CO_2 concentration (µmol CO_2 mol^{-1})	Bulb yield (t ha^{-1})
Ekfutia Assam	1.90	1.14	21.51	0.50	68.20	309.17	10.03
Assam Local	1.59	1.07	18.17	0.52	59.29	312.75	8.63
Bhima Omkar	1.70	0.87	17.68	0.57	60.53	309.55	10.05
Bhima Purple	1.63	0.89	16.68	0.54	63.45	316.51	8.86
S. Ed.	0.03	0.02	0.63	0.01	4.35	2.21	0.06
CD (0.05%)	0.07	0.03	1.34	0.02	9.23	4.69	0.13

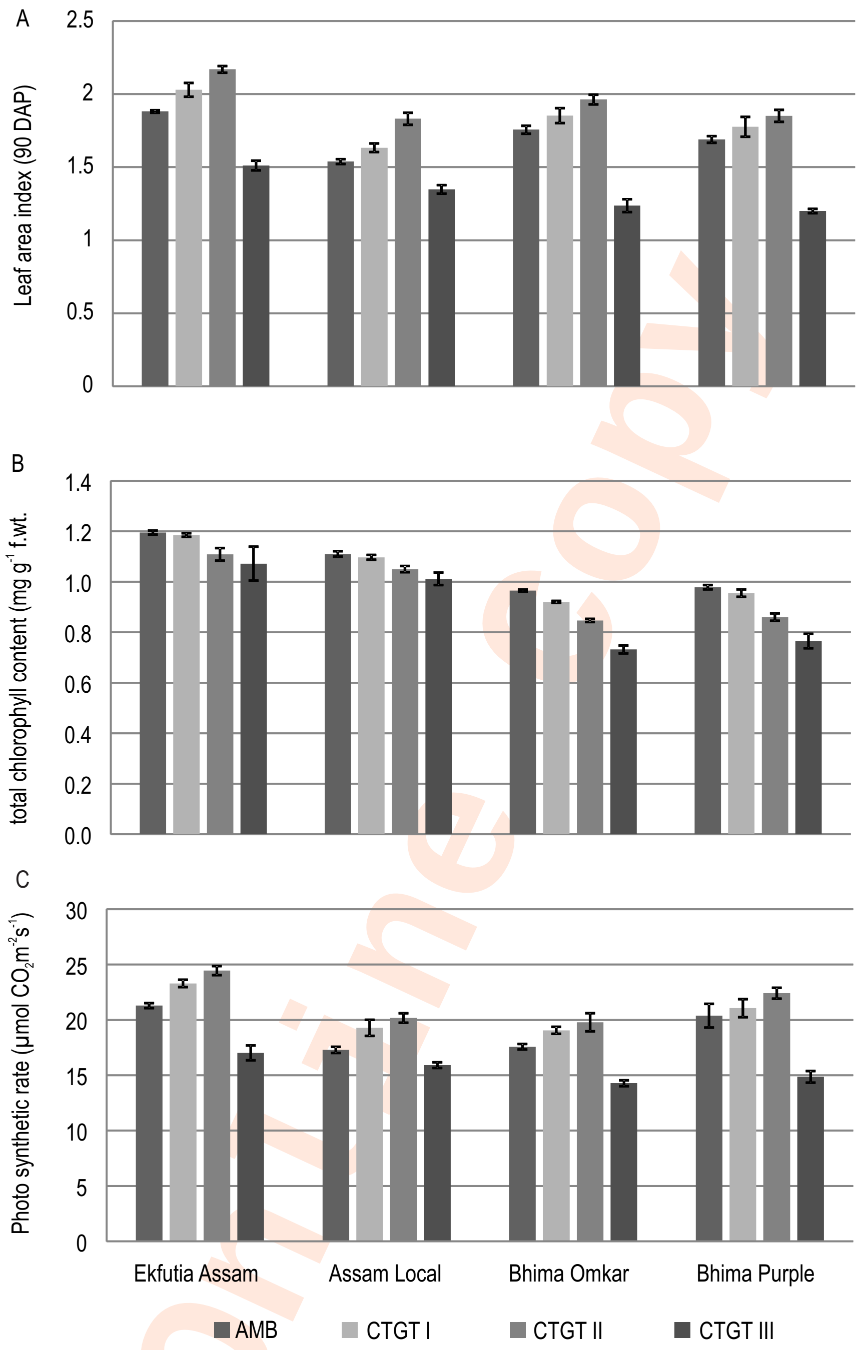

Fig. 1: Interactive effect of elevated CO_2 and temperature on Leaf area index 90 DAP (A); Total Chlorophyll content (B) and Photosynthetic rate (C) in four selected varieties of garlic (*Allium sativum*).

like Ekfutia Assam and Assam Local, under Carbon dioxide Temperature Gradient Tunnel-II (Table 1) maintained a good amount of chlorophyll which helped in photosynthetic process and less reduction percent was observed in Carbon dioxide Temperature Gradient Tunnel-II as compared to Carbon dioxide Temperature Gradient Tunnel-III (Fig.1B).

The total chlorophyll content of leaves was reduced under higher CO_2 concentration. The total chlorophyll content decreased as compared to garlic plants grown under ambient condition to the tune of 2.16% in Carbon dioxide Temperature Gradient Tunnel-I, 9.02% in Carbon dioxide Temperature Gradient Tunnel-II and 15.73% in Carbon dioxide Temperature Gradient Tunnel-III. This

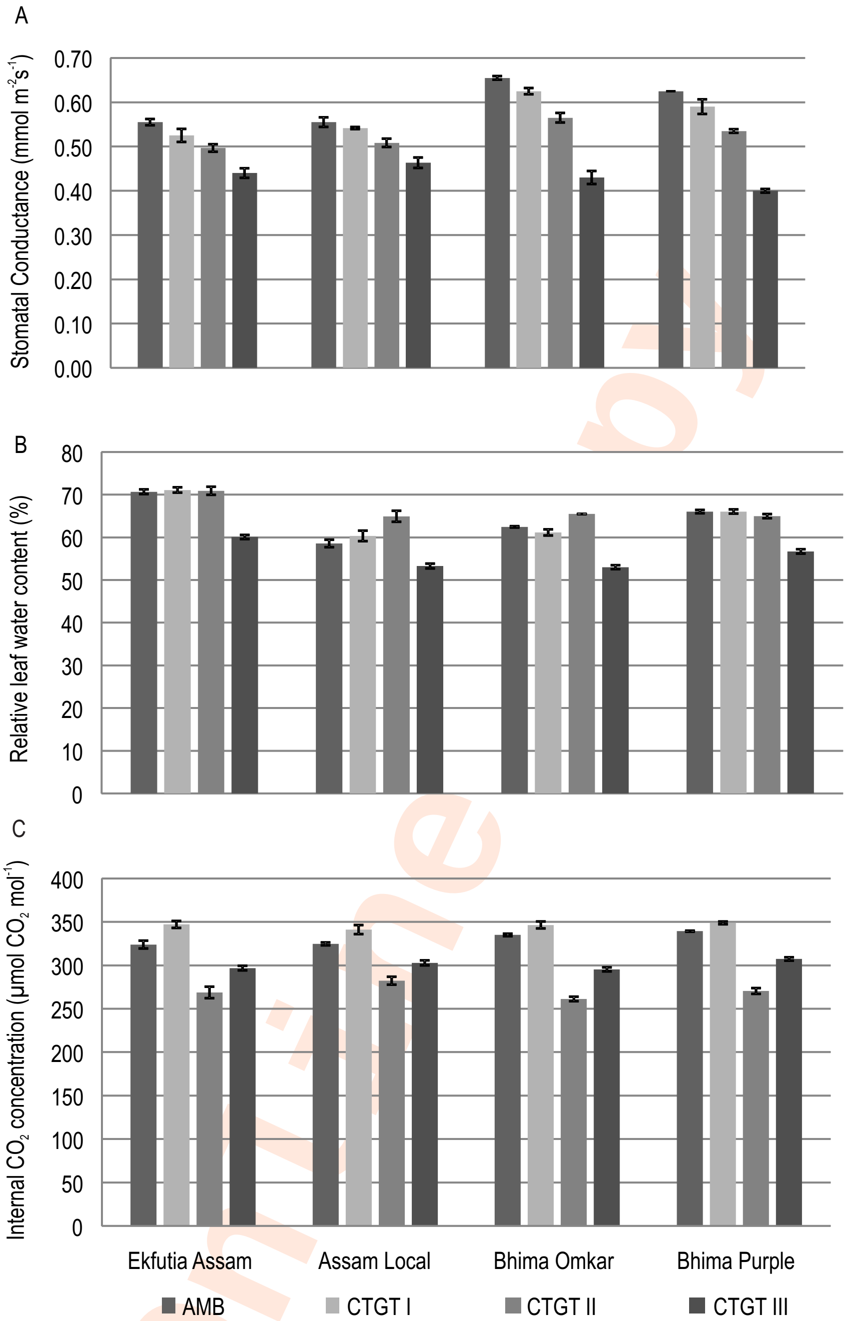

Fig. 2: Interactive effect of elevated CO_2 and temperature on Stomatal Conductance (A), RLWC (B), Internal CO_2 concentration and (C) of four selected varieties of garlic (*Allium sativum*).

finding is in accordance with the findings of Faria *et al.* (1996) and Jobe *et al.* (2020) who reported that the concentration of total chlorophyll content showed a small increase under elevated CO_2 on leaf area basis, but it decreased significantly on dry weight basis as a result of the decrease in specific leaf area in elevated plants. Wullschleger *et al.* (1992) observed the reduction in chlorophyll and accessory pigments under elevated CO_2 condition. High temperature stress adversely affected the chlorophyll concentration in leaves. However, this reduction in chlorophyll content was ameliorated by enrichment of CO_2 which led to slow degradation; however, significant variations were observed among the varieties. The highest chlorophyll content was recorded in the variety Ekfutia Assam followed by Assam Local, indicating the maintenance of chlorophyll in these varieties

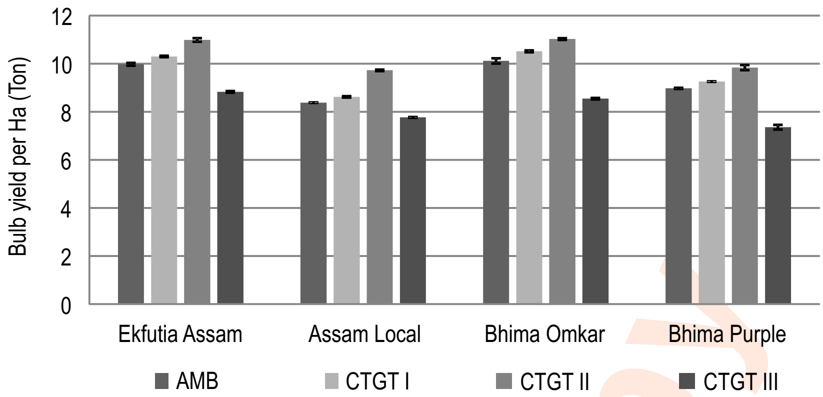

Fig. 3: Interactive effect of elevated CO_2 and temperature on yield of four selected varieties of garlic (*Allium sativum*).

under Carbon dioxide Temperature Gradient Tunnel-II (Table 2). Two year pooled data on photosynthetic rate of all the four varieties recorded highest in Carbon dioxide Temperature Gradient Tunnel-II which was13.43% higher over varieties under ambient condition (Table 2). The interaction effect of varieties and concentrations of CO_2 and temperatures on photosynthetic rate was found to be significant (Fig. 1C).The highest increase of 16.64% in the photosynthetic rate was recorded in Assam Local under Carbon dioxide Temperature Gradient Tunnel-II whereas, there was reduction in photosynthetic rate in Carbon dioxide Temperature Gradient Tunnel-III by 7.97%. These evidences substantiate the existence of significant genotypic variation for photosynthetic potential across garlic varieties. Differential photosynthetic responses were observed by Zheng *et al*. (2019) in soybean. These responses may be either positive or negative depending upon the species due to the down regulation or up regulation of photosynthetic activity under elevated level of CO_2 (Reddy *et al*., 2010).

The increase in photosynthetic rate on enrichment of CO_2 may be attributed to the increase in water use efficiency in plant tissue as explained by Nackley *et al.* (2016). At Carbon dioxide Temperature Gradient Tunnel-II with 550 ppm CO_2 + 4°C higher temperature than ambient, significant increase of 13.43% in the rate of photosynthesis was recorded in Ekfutia Assam over ambient condition (Table 2). High temperature stress treatment led to reduction in the photosynthetic rate. However, this detrimental effect was lesser under Carbon dioxide Temperature Gradient Tunnel-II (21.71 µmol CO_2 $m^{-2}s^{-1}$) in comparison to Carbon dioxide Temperature Gradient Tunnel-III (15.52 µmol CO_2 $m^{-2}s^{-1}$) which might be due to the ameliorative effect of enhanced CO_2 level. Nackley *et al.* (2016) also reported that fleshy leaf scales of garlic are better adapted to increased level of CO_2 which raised the photosynthetic rate even under high temperature.

In the present investigation, the varieties Assam Local recorded least reduction in total chlorophyll content among the four varieties grown under observation in Carbon dioxide Temperature Gradient Tunnel-II at -5.41%. Similarly, the least per cent reduction in chlorophyll content (8.86%) was recorded in the variety Assam Local in Carbon dioxide Temperature Gradient Tunnel-III, indicating maintenance of chlorophyll content better by this variety under given stress condition. Significant increase in the mean relative leaf water content was recorded in Carbon dioxide Temperature Gradient Tunnel-II (66.58%) as compared to four varieties grown under ambient condition (64.44%) which was ascertained by 10.60% increase in photosynthetic rate-grown under Carbon dioxide Temperature Gradient Tunnel-II as compared to ambient condition (Table 1), however, drastic reduction in relative leaf water content was recorded in relative leaf water content–III, which was again ascertained by drastic reduction in photosynthesis rate in relative leaf water content-III over ambient condition. The increase in photosynthesis may be attributed to the maintenance of higher level of water content in the leaves of garlic plant and reduction in transpiration rate (Acock and Allen, 1985). According to Uprety *et al.* (1998) and Morinaga (2002), the inherent sink strength of plant helps in directing the response of leaves to an elevated CO_2 concentration.

Elevated CO_2 has positive stimulation on plant growth which increases the photosynthetic rate and maintains stomatal conductance, enhancing carbon gain while reducing water loss (Kirkham, 2011; Yu *et al.,* 2012; Haworth *et al.,* 2016). Similar findings were also recorded in the present investigation. The interaction effects recorded least reduction of stomatal conductance (Fig. 2A) in variety Assam Local in both relative leaf water content-III (-16.52%) and relative leaf water content-II (-8.41%). The reduction in photosynthetic rate due to combined effect of both higher concentration of CO_2 and temperature stress (relative leaf water content-III) may be attributed to lower consumption of internal CO_2 concentration, however, under relative leaf water content-II it was highly ameliorated by CO_2 enrichment. But in relative leaf water content-III under 700 ppm of CO_2 and 6°C temperature stress, stomatal conductance was distorted, which indicated that stomata are one of the integral part for carbon uptake in plants. Qaderi *et al.* (2006) and Ge *et al.* (2012) also provided similar reports of depression in stomatal conductance under relevated CO_2 and temperature stress. Elevation in CO_2 concentration enhanced the net photosynthetic rate and decreased stomatal conductance thus, resulting in higher water use efficiency in *Olea europaea*, (Sebastiani *et al.,* 2002). The highest internal CO_2 content was observed in relative leaf water content-I, which was 15.17% higher than ambient on average for all the four varieties under investigation. The same parameter was recorded lowest in relative leaf water content-II. The maximum increment in internal CO_2 concentration content due to stress treatment in Carbon dioxide Temperature Gradient Tunnel-I was recorded in the variety Ekfutia Assam (7.15%) followed by Assam Local (5.08%). Similarly, the reduction in internal CO_2 concentration content was lowest in Assam Local (-13.04%), followed by Ekfutia Assam (17.01%) in Carbon dioxide Temperature Gradient Tunnel-II depicting their better adaptability to stress condition (Fig. 2 C).

Relative water content recorded an increasing trend in all the varieties on increase in CO_2 concentration and temperature from 64.44% in ambient condition to 66.78% in Carbon dioxide Temperature Gradient Tunnel-II. Nackley *et al.* (2016) reported that improvement in water use efficiency of garlic plants resulted in increased carbon per unit water used under elevated CO_2 concentration. This is of utmost importance with regard to the changing climatic conditions of increased temperature and decreased fresh water supplies. In this context, tolerant varieties which have some capacity to maintain water potential might adapt even at elevated CO_2 level of 550 ppm. However, the highest increase in relative water content over ambient was recorded in Assam Local at 10.88% (64.94%) in Carbon dioxide Temperature Gradient Tunnel-II. The increase in relative water content provides turgor required for cell expansion the helps in enhancing plant growth and development characters leading to accumulation of substrates in bulb, thereby increasing the yield (Nackley *et al.,* 2014).

Similarly 3.41% and 11.11% increase in bulb yield (t ha^{-1}) was recorded in Carbon dioxide Temperature Gradient Tunnel-I and Carbon dioxide Temperature Gradient Tunnel-II respectively over crop grown under ambient condition. The interactive effect of higher CO_2 concentration and higher temperature showed highest per cent increase in yield in case of Assam Local (16.01%) followed by Ekfutia Assam (10.15%) in Carbon dioxide Temperature Gradient Tunnel-II compared to the yield obtained for the varieties grown under ambient condition. The highest level of CO_2 and temperature in Carbon dioxide Temperature Gradient Tunnel-III were found to affect almost all major physiological parameters, including production of garlic bulbs in a negative way. However, the reduction in yield was recorded least in Assam Local (-7.33%) followed by the variety Ekfutia Assam (-11.48%) under CTGT-III. It could be opined that a moderate increase in CO_2 concentration with temperature has some positive impact on physiological parameters of plants. There was variability among genotypes in terms of growth and yield response under higher level of CO_2 and temperature. High temperature significantly decreased yield and yield attributing characters but increased levels of CO_2 (550 ppm) helped in ameliorating its negative effect. Genotypes, Assam Local and Ekfutia Assam responded positively under elevated CO_2 and high temperature conditions and produced better yield compared to other varieties like Bhima Omkar and Bhima Purple.

It can be concluded that Assam local and Ekfutia Assam had some degree of tolerance against higher level of CO_2 and temperature and this could be attributed to higher photosynthetic rate and adjustment of water relation parameters like relative water content and modification of stomatal conductance and some morphological parameters like leaf area, yield, *etc*. Hence, genotypes Assam Local and Ekfutia Assam can be utilized in changing climatic conditions for sustainable productivity. It can also be used as breeding material for development of stress resistant variety in near future. The present investigation might help in achieving high production with improved qualities of garlic in the near future to meet the rising demand of consumers by 2025.

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Add-on Information

Authors' contribution: N. Rahman: Conducted experiment, Data collection, compilation, analysis and interpretation; **R. Das:** Planning and Design of experiment and interpretation; **B.D. Narzary, D.B. Phookan, A. Saikia:** Planning and Design of experiment and interpretation; **S. Alam:** Data analysis and interpretation.

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