Elevated CO$_2$ and Temperature Resetting the Expression of Resistance, Pest Incidence, Geographical Distribution and Physiology in Insect-pests of Grain Legumes: A Review

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ABSTRACT

The most important factor that affects the crop production in terms of nutritional content of foliar plants is the global climate change. Herbivore's growth, development, survival and geographical distribution all are determined by elevated CO$_2$ and temperature. The interactions between herbivores and plants have changed due to increasing level of CO$_2$ and temperature. The effect of high CO$_2$ and temperature on grain legume plant which change in to plant physiology (*e.g.*, nutritional content, foliage biomass) and how it change in herbivory metabolism rate and food consumption rate. Plant injury is determined by two factors *viz.* resistance and tolerance and both are influenced by greater CO$_2$ and temperature. Legumes are an important source of food and feed in the form of proteins and also improve the soil environment. The repercussions of the abiotic factors mentioned above needs discussion among the scientific community. We may able to limit the negative repercussions of stated factors in future breeding projects by harnessing the practical favourable impacts and by including such influences of elevated CO$_2$ and temperature on pulses productivity. The extensive research is necessary to overcome the negative effects of high CO$_2$ and temperature on insect-plant interaction.

Key words: Elevated CO$_2$, Host-plant interaction, Legumes, Resistance, Temperature.

CO$_2$ level in the atmosphere is currently about 406.94 parts per million (ppm) on a worldwide scale (Anon, 2017). In the last 250 years, atmospheric CO$_2$ concentration has risen from 280 to 390ppm and by the end of 2050, it expected to rise at least 550ppm (IPCC, 2007). As an abiotic element, it affects the expression of plant resistance (Lindroth, 2010; Robinson *et al.*, 2012). Elevated level of CO$_2$ increases the C:N ratio, which lowers the nitrogen concentration in the tissues of most plant species, making them more sensitive and affecting the feeding habits of insect-pest species (Bezemer *et al.*, 2000; Sun *et al.*, 2010; Couture *et al.*, 2010; Guo *et al.*, 2014). To balance this ration, the phytophagous animals would consume more foliage and therefore, more damage to crop plants (Bezemer and Jones, 1998). Variations in climatic change have a significant impact on pest abundance and dispersion (McKenzie and Andrews, 2010; Sharma, 2014). Alteration in CO$_2$ concentration also results in biochemical and morphological changes (Robinson *et al.*, 2012) and that plays vital role in plant defence mechanism of host plant resistance to insect pests (War *et al.*, 2012, 2013). Generally the plant develops many strategies to defend itself against the negative impacts of foliar feeders (Strauss and Agrawal, 1999; Fornoni *et al.*, 2003). Plants respond by producing repellents or defensive elements so to reduce the effect of pest species (Halitschke and Baldwin, 2004). Elevated CO$_2$ also alters the activity of plant oxidative enzymes such as peroxidase (POD), polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL), tyrosine ammonia lyase (TAL), superoxide dismutase and catalase in the host plant (Badiani *et al.* 1993; Polle *et al.* 1997). The photosynthetic rate, which is regulated by

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ambient CO$_2$ level, has a significant impact on the physiology and biochemical composition (C:N ratio) of plant foliage, as well as the allocation of these components of plant leaves (Long *et al.*, 2004). When wild tomato plants are grown and fed under elevated CO$_2$, the activities of total protease, trypsin-like enzymes and weak and active alkaline trypsin-like enzymes increased in the midgut of the cotton bollworm, *Helicoverpa armigera* (Hubner) (Guo *et al.*, 2012). The negative impact of elevated CO$_2$ level on insect physiology has been investigated (Akbar *et al.*, 2016). The development and physiology of herbivorous insects are affected by the changes in food quality (Khadar *et al.*, 2014). Sharma *et al.* (2016a) investigated the effect of increased CO$_2$ on plant defense response in chickpea against *Helicoverpa armigera* and found increase in total phenols and condensed tannins. Tannins in plant foliage can protect against foliage feeder

by making the plant toxic or deterring the insects from feeding on it (Barbehenn and Constabel, 2011). Hydrogen peroxide, oxalic and malic acid level were higher in *H. armigera*-infested plants at 750 ppm than at 350 ppm CO$_2$ level (Sharma *et al.*, 2016b). The primary goal of this review paper was to determine the impact of increased CO$_2$ concentration and temperature on resistance expression, pest damage and insect development in grain legumes.

Elevated CO$_2$ and temperature *vs* pest incidence and geographical distribution

According to the third IPCC study, global average surface temperature is expected to rise by 1.4°C to 5.8°C by 2100 and after it will rise even more fast (Houghton *et al.*, 2001). During the last 1,000 years, the rise in temperature in the twentieth century has been the most serious problem of any century. As a result of global warming, pest outbreak have become more common and severe (Sharma, 2014). The pest population became unstable due to rising CO$_2$ level and resulted in severe outbreak of pest species (War *et al.*, 2016). Regional distribution, abundance, seasonal incidence and intensity of few pests got shifted due to elevated CO$_2$ level (Menendez, 2007; IPCC, 2014; Sharma, 2014). Change in climate fastens the severe outbreak of *H. armigera* and *Maruca vitrata* in legume crops (Sharma, 2005; Sharma, 2010). Among all the abiotic climatic variations, the extreme range of temperature has a significant impact on phytophagous herbivore distribution (Boullis *et al.*, 2015). More potential of new pests and pest niches arise when the average temperature rises. Pod infestation by *H. armigera* and *M. vitrata* in pigeonpea crops varies and it depends the temperature at different planting dates (Jat *et al.*, 2021; Jat *et al.*, 2018a) (Table 1). In the pigeonpea crop, higher temperature results in a greater larval population as well as a higher incidence of *H. armigera* and *M. vitrata*. The larval population of *H. armigera* was positively correlated with the higher temperature (Jat *et al.*, 2017). Furthermore, the occurrence of insect pests in pigeonpea and chickpea crops also varied in different months (Sharma *et al.*, 2016b). In September and January seeded pigeonpea and chickpea

crops, the crop damage was appreciably high due to infestation by *H. armigera* and *Spodoptera exigua* (Hub.) (Sharma *et al.*, 2016b).

Effect of elevated CO$_2$ and temperature on foliage consumption and insect development

Nitrogen is one of the most critical limiting factors for phytophagous herbivores (Mattson, 1980). Decrease in the foliar nitrogen content of the host plant may impair the development and survival rates of phytophagous insects. Variability in climatic variables weakens the plant's defence against herbivorous insects by virtue of the fact that nitrogen is the most abundant component of proteins (Khadar *et al.*, 2014; Sharma, 2016) and a limiting element for insect-pest reproduction and performance (Lindroth *et al.*, 1993; Shwetha *et al.*, 2019). Therefore, decrease in leaf nitrogen content under elevated CO$_2$ concentration results in plant nitrogen deficit (Lindroth *et al.*, 1993). Feeding such plants would enhance the leaf consumption and duration of development (Feng *et al.*, 2010). For instance, the chickpea plant grown in high CO$_2$ concentration has decreased protein content in their tissues, making them nutritionally deficient (Khadar *et al.*, 2014). *H. armigera* needs more protein for proper growth and development and it will strive to compensate by consuming as much as possible. Carbon dioxide also reduced the plant's ability to defend itself against phytophagous insects (Zavala *et al.*, 2008). Coviella and Trumble (1999) and Sharma *et al.* (2016b) hypothesized that plants grown under higher CO$_2$ and temperature level are less nutritious and herbivores will increase their feeding time and foliage consumption.

Insect development and physiology directly influenced by temperature fluctuations, with equivalent impacts on the nutritional composition of host plants (Ayres and Scriber 1994). Hunter (2001) and Yadugiri (2010) investigated the direct and indirect effects of temperature and CO$_2$ on insect growth. In general, rising temperature leads to a higher survival rate and a shorter life cycle (Bale *et al.* 2002). Increasing in plant dry biomass and C:N ratio, longer main stem length, elongation of branches, individual leaf area

Table 1: Correlation coefficient between *H. armigera* and *M. vitrata* population and abiotic factors in different sowing dates.

Weather parameters	*H. armigera*				*M. vitrata*			
	D$_1$	D$_2$	D$_3$	D$_4$	D$_1$	D$_2$	D$_3$	D$_4$
Max T	0.626**	0.162	0.743*	-0.248	0.146	-0.200	0.704*	-0.340
Min T	0.537*	0.160	0.574	-0.067	-0.175	-0.653*	0.476	-0.179
AVP I	0.518*	0.087	0.500	0.019	-0.255	-0.688*	0.414	-0.104
AVP II	0.384	0.042	0.374	0.111	-0.405	-0.762**	0.312	-0.017
RH - I	-0.345	-0.038	-0.245	0.330	-0.139	0.274	-0.399	0.422
RH - II	0.118	-0.092	0.080	0.912**	-0.671**	-0.586*	-0.564	0.906*
WS (Km/h)	0.109	-0.189	0.389	-0.087	-0.533*	-0.829**	0.149	-0.160
BSS (Hrs)	0.476	-0.228	0.090	-0.278	0.163	0.091	0.496	-0.384
PAN (mm)	0.420	-0.136	0.414	-0.196	-0.164	-0.374	0.392	-0.289
Rainfall (mm)	-0.059	-0.377	0.829**	0.186	-0.552*	-0.454	0.282	0.219

D$_1$: (3rd week of June); D$_2$: (1st week of July); D$_3$: (2nd week of July); D$_4$: (3rd week of July).

per plant and reduced foliar nitrogen are the results of increased CO$_2$ sensitivity in C$_3$ plants (Chen *et al*., 2005a; Shwetha *et al*., 2019). Increased CO$_2$ (550ppm) results in significantly greater leaf area, root dry weight and total dry matter accumulation in French bean plants (Rao *et al*., 2015). Because of CO$_2$ fixation mechanisms, leguminous crops respond positively to elevated CO$_2$ level and results in increased biomass output among C$_3$ plants (Kimball *et al*., 2002). Some mungbean genotypes have a beneficial attributes with increased CO$_2$ concentrations (570-20ppm) (Haque *et al*., 2005).

The drop in leaf N content caused by quicker growth of the foliage plants stimulated photosynthesis and growth in plants growing under elevated CO$_2$ circumstances (Stitt and Krapp, 1999). Under high CO$_2$, the leaf N content of legume crops reduced by an average of 7% (Cotrufo *et al*., 1998). Rao *et al*. (2012) found an 8% drop in leaf N content under increased CO$_2$ concentrations when compared to ambient CO$_2$. The foliar nitrogen concentration of the plant decreases as CO$_2$ level rises and results in 40% higher food consumption by herbivores (Sharma *et al*., 2016b; Chen *et al*., 2005b).

The nutritional composition of the plant became altered by increased CO$_2$ concentration and temperature, which might make the foliage plant unpleasant or nutritionally better for the insects (Sterner and Elser, 2002). Lower level of leaf nitrogen, higher carbon, higher relative proportions of carbon to nitrogen and higher polyphenols content have been recorded in groundnut plants cultivated under elevated eCO$_2$ (550 ppm and 700 ppm) level. When compared to ambient CO$_2$ level, leads to longer larval duration, greater larval weight and increase intake of groundnut plant leaf (Rao *et al*., 2012; 2014). Similarly, groundnut foliage grown in eCO$_2$ circumstances has reduced leaf nitrogen content, greater carbon and a higher C:N ratio (Shwetha *et al*., 2019).

Increased temperature causes a faster rate of development in arthropods and results in more generations per year and a wider geographical dispersion (Parmesan *et al*., 1999; Bale *et al*., 2002; Sharma 2014). When *Helicoverpa armigera* larvae were reared under elevated CO$_2$, larval survival, larval weight, larval period, pupation and adult emergence were all negatively affected, whereas pupal weight, pupal period and adult fecundity were improved (Akbar *et al*., 2016). In brief, the growth and development, reproduction and survival of of *H. armigera*, were strongly influenced by rising temperature and precipitation (Sharma, 2014). Similarly, when the larvae of *Spodoptera litura* feed on groundnut plants with eCO$_2$ values (550ppm and 700ppm), showed a longer larval duration and larval weight (Rao *et al*., 2014). On the contrary, with elevated CO$_2$ concentrations (732.1±9.99 µl/liter), larval and pupal weights of *S. litura* were significantly reduced, but the duration of larval and pupa on soybean were significantly increased (Yifei *et al*., 2018).

Adati *et al*. (2004) investigated the effect of temperature on the development and survival of the legume pod borer,

Maruca vitrata, under the *in vivo* condition. The developmental time for eggs, larvae and pupae reduced with increasing temperature from 14.4°C to 29.3°C. For development of egg, larval and pupal stages, the thermal constant and lower thermal threshold were 51.1, 234.7 and 116.5 degree-days and 10.5, 10.0 and 10.9°C, respectively.

The aphid population on soybean plants was considerably greater after 1 week under elevated CO$_2$ (550 L/L) concentrations, with populations twice the size of plants cultivated under ambient CO$_2$ level (O'Neill *et al*., 2011). Similarly, higher temperature has a detrimental impact on larval survival, larval duration, pupal weight and pupal period, but has a positive impact on larval growth. Increased metabolic rate may be responsible for increased larval growth (Bale *et al*., 2002; Jamieson *et al*., 2012). Increased food consumption and metabolism of *H. armigera* larvae were observed when CO$_2$ and temperature levels were enhanced (Akbar *et al*., 2016). This is due to increased activity of midgut protease, amylase and cellulose (carbohydrates) and mitochondrial enzymes. When larvae were reared under elevated CO$_2$ concentration compared to ambient CO$_2$ level, Khadar *et al*. (2014) found that food consumption rose by 81.67 percent. The food consumption of *S. litura* was maximum (3758.07 mg) during its whole life cycle when exposed to eCO$_2$ + eTemperature (550 ppm + 2°C) (Shwetha *et al*., 2019). In line, Wu *et al*. (2006) observed similar observations. Yifei *et al*. (2018) proposed that elevated CO$_2$ level promote an increase in the amount of feeding and excretion of soybean plants by *S. litura*.

Chickpea plants cultivated at high CO$_2$ level (550ppm and 700ppm) exhibited low nitrogen and high carbon content and that has led to increased food consumption by *H. armigera*, which in turn increased larval weight and increased the excreta (Khadar *et al*., 2014). More damage to chickpea plants is the result of no change in phenol content, more approximate digestibility and more relative consumption rate by the larva under elevated CO$_2$ as compared to ambient CO$_2$ level. The nutritional quality of mungbean leaves was reduced due to dilution of nitrogen content under elevated CO$_2$ level, resulting in increased feeding capacity of *S. litura* (Srivastava *et al*., 2002). As atmospheric CO$_2$ level goes up, it may decrease nitrogen concentration and high non-structural carbohydrate level. This climatic change may alter the plant-herbivore interaction, as well as *S. litura* feeding habits.

Elevated CO$_2$ *vs* change in morphological and biochemical components

Hunter (2001) has clearly established the effect of increased CO$_2$ concentration on plant phytochemistry. Climate change, particularly changes in CO$_2$ and temperature regimes have a significant impact on host-plant resistance mechanisms (Sharma *et al*., 2016b) (Table 2 and 3). The photosynthetic route determines the growth and development as well as the biochemical contents of plants cultivated in high CO$_2$ environment. Groundnut and chickpea plants grown in CO$_2$ (550 ppm) had a considerable drop in leaf nitrogen and

Table 2: Amounts of phenols (mg TAE/g FW), tannins (mg CE/g FW) and chlorophyll (µg cm^{-2}) content of chickpea plants infested with *Helicoverpa armigera* under different CO_2 regimes.

CO_2 (ppm)	ICCL 86111		JG 11	
	Un-infested	Infested	Un-infested	Infested
Total phenols				
350 ppm	15.8±0.05[a]	17.85±0.08[a]	12.67±0.07[a]	13.84±0.12[a]
550 ppm	16.2±0.71[a]	19.31±0.07[a*]	14.47±0.10[ab]	15.92±0.14[ab]
750 ppm	16.9±0.27[a]	19.70±0.08[a*]	14.78±0.20[ab]	16.03±0.14[ab]
Ambient conditions	16.5±0.67[a]	18.49±0.67[a]	15.35±0.45[b]	17.50±0.91[b]
Mean	16.35	18.83	14.32	15.82
Tannins				
350 ppm	9.41±0.15[a]	11.85±0.48[a]	9.41±0.98[a]	10.60±0.52[a]
550 ppm	10.40±0.17[a]	12.60±0.74[a*]	10.40±0.30[a]	11.82±0.74[a*]
750 ppm	10.47±0.99[a]	11.70±0.58[a]	9.78±0.29[a]	11.23±0.84[a*]
Ambient conditions	9.90±0.97[a]	12.11±0.92[a*]	8.4±0.34[a]	10.2±0.79[a]
Mean	10.05	12.07	9.49	10.96
Chlorophyll				
350 ppm	28.6±1.15[b]	28.15±2.41[ab]	17.20±1.91[ab]	30.22±2.55[c]
550 ppm	27.83±1.70[b]	23.30±1.97[a*]	30.17±2.30[c]	19.65±1.71[a]
750 ppm	17.35±1.39[a]	21.65±1.58[a*]	14.95±1.20[a]	17.78±1.08[a]
Ambient conditions	29.53±2.09[b]	29.53±2.09[ab]	21.85±1.94[b]	29.53±2.13[b]
Mean	25.82	25.66	21.04	24.29

Values (means ± SE) with the same letter within a column are not significantly different at $p \leq 0.05$.
*Values within a row across the infested and un-infested plants are significantly different at $p \leq 0.05$.

Table 3: Carbohydrate and protein content of chickpea plants infested with *Helicoverpa armigera* under different CO_2 regimes.

CO_2 (ppm)	ICCL 86111		JG 11	
	Un-infested	Infested	Un-infested	Infested
Chlorophyll content (mg/0.1 g leaf tissue)				
350 ppm	33.6±3.12[a]	34.4±2.50[b*]	33.6±1.45[a]	35.2±1.56[a*]
550 ppm	44.0±2.00[b]	27.2±1.25[ab*]	40.0±2.00[b]	27.2±1.23[*]
750 ppm	48.0±1.50[b]	24.0±2.20[a*]	44.8±2.22[bc]	24.8±1.56[a*]
Ambient conditions	33.6±2.52[a]	20.8±1.09[a*]	26.8±1.20[a]	19.6±1.72[a*]
Mean	39.80	26.6	38.8	27.0
Protein (mg/g leaf tissue)				
350 ppm	49.5±1.48[b]	33.0±1.50[a*]	48.0±1.82[c]	30.3±2.00[a*]
550 ppm	45.0±1.80[b]	39.0±2.97[ab*]	42.0±1.24[b]	32.0±2.12[a*]
750 ppm	33.0±1.50[a]	40.0±3.83[b*]	33.0±1.50[a]	36.0±2.12[a]
Ambient conditions	46.0±2.56[b]	42.1±2.56[b]	40.0±2.70[b]	42.0±2.10[b]
Mean	43.38	38.53	40.75	35.0

Values (means ± SE) with the same letter within a column are not significantly different at $p \leq 0.05$.
*Values within a row across the infested and un-infested plants are significantly different at $p \leq 0.05$.

protein, whereas the carbon C:N ratio, phenols and tannin content were much greater in CO_2 (550 ppm) and least in ambient concentration (Shwetha *et al.*, 2019; Khadar *et al.*, 2014). Elevated temperature seems to reduce the morphological and biochemical components of the pigeonpea resulting in increasing damage by pod borer (Jat *et al.*, 2018a; Jat *et al.*, 2021). (Table 4). In comparison to June sown pigeonpea genotypes to July or August sown genotypes, the phenol content and condensed tannins were found higher (Jat *et al.*, 2018b) (Table 5 and 6). Such

changes have led to the pod borer infestation in the pigeonpea. The mean phenol content of chickpea plants infested with *H. armigera* was substantially higher than that of uninfested plants (Sharma *et al.*, 2016b). Under elevated CO_2 concentration (550 and 750ppm), the activity of phenylalanine ammonia lyase (PAL), tyrosine ammonia lyase (TAL), total phenols and condensed tannins were increased in chickpea plants (Muzika, 1993; Sharma *et al.*, 2016b). Increasing activity of these compounds affects the expression of plant resistance to foliage feeders. Several

studies have found that high temperature diminish the expression of genes influencing wheat resistance to several biotypes of the Hessian fly, *Mayetiola destructor* (Tyler and Hatchett, 1983). Certain environmental conditions, particularly temperature, have an impact on the success of transgenic crops in pest management (Sharma 2014). This elevated condition changes the interaction between insect pests and their host plants.

Increased CO$_2$ concentration could reduce photorespiration in C$_3$ photosynthesis and makes photosynthesis more efficient. But the foliar nitrogen and protein concentrations dropped more than 12% (Ainsworth and Long 2005). According to Dermody *et al.* (2008) higher CO$_2$ level alone and in combination with O$_3$ increased the abundance of western corn rootworm,

Diabrotica virgifera adults (foliage chewer) and soybean aphids, *Aphis glycines* (phloem feeder), as well as the amount of leaf area damage in the soybean agroecosystem. At excessive CO$_2$ concentration (550), the Japanese beetle, *Popillia japonica*, significantly increased the foliage damage to soybean plants. Maximum consumption of leaf was observed among the beetle was observed when the temperature was raised to 37° C (Niziolek *et al.*, 2013). The nutritional value of plants is greatly reduced due to loss of nitrogen and protein, influencing the growth and development of insect herbivores either directly or indirectly. On the other hand, plants using C$_4$ pathway of photosynthesis will have poor response to increased atmospheric CO$_2$ due to photosynthetic saturation (Leon and Vara, 2004).

Table 4: Per cent pod infestation by major pod borer complex in different pigeonpea varieties and different sowing dates.

Borer complex	Sowing	Varieties						Mean
		Paras	Manak	AL-201	Pusa-992	AL-881	H03-41	
H. armigera	D$_1$	3.92(11.41)	3.40(10.62)	2.62(9.31)	4.34(12.02)	3.46(10.71)	3.65(11.00)	3.56(10.85)
	D$_2$	5.64(13.71)	3.60(10.87)	3.41(10.59)	4.45(12.17)	5.58(13.63)	4.56(12.25)	4.54(12.20)
	D$_3$	2.00(8.12)	5.51(13.33)	2.42(8.90)	4.07(11.41)	3.27(10.10)	1.84(7.70)	3.18(9.93)
	D$_4$	1.39(6.75)	2.32(8.75)	1.33(6.63)	2.02(8.02)	2.06(8.24)	1.07(5.73)	1.70(7.35)
Mean		3.24(10.00)	3.71(10.89)	2.45(8.86)	3.72(10.90)	3.59(10.67)	2.77(9.17)	
S.Em.±	Factor A	(Dates of sowing)					0.34	
	Factor B	(Varieties)					0.42	
	Factor A × B	(Dates of sowing × varieties)					0.84	
CD	Factor A	(Dates of sowing)					0.97	
P = (0.05)	Factor B	(Varieties)					1.19	
	Factor A × B	(Dates of sowing × varieties)					2.37	
M. vitrata	D$_1$	3.23(10.35)	3.35(10.51)	1.58(7.19)	3.69(11.07)	3.52(10.80)	2.19(8.45)	2.93(9.73)
	D$_2$	14.86(22.66)	13.44(21.49)	9.29(17.74)	15.62(23.27)	13.92(21.90)	11.37(19.70)	13.08(21.12)
	D$_3$	3.81(11.25)	6.25(14.46)	2.79(9.61)	10.73(19.11)	2.58(9.24)	3.17(10.19)	4.89(12.31)
	D$_4$	2.00(8.10)	1.97(8.00)	3.53(10.82)	1.57(7.18)	3.59(10.89)	1.18(6.19)	2.30(8.53)
Mean		5.97(13.09)	6.25(13.61)	4.30(11.34)	7.90(15.16)	5.91(13.21)	4.48(11.13)	
S.Em.±	Factor A	(Dates of sowing)					0.19	
	Factor B	(Varieties)					0.23	
	Factor A × B	(Dates of sowing × varieties)					0.47	
CD	Factor A	(Dates of sowing)					0.55	
P = (0.05)	Factor B	(Varieties)					0.66	
	Factor A × B	(Dates of sowing × varieties)					1.33	
M. obtusa	D$_1$	1.87(7.87)	3.21(10.29)	1.36(6.67)	1.96(8.05)	1.80(7.67)	1.97(8.05)	2.03(8.10)
	D$_2$	3.26(10.39)	2.22(8.55)	2.08(8.29)	2.99(9.95)	2.24(8.60)	2.69(9.44)	2.58(9.20)
	D$_3$	2.46(9.02)	2.65(9.34)	1.24(6.39)	2.72(9.49)	2.75(9.54)	1.72(7.52)	2.26(8.55)
	D$_4$	2.29(8.64)	2.79(9.59)	1.74(7.58)	1.50(6.94)	3.77(11.11)	0.63(4.48)	2.12(8.06)
Mean		2.47(8.98)	2.72(9.44)	1.61(7.23)	2.29(8.61)	2.64(9.23)	1.75(7.37)	
S.Em.±	Factor A	(Dates of sowing)					0.18	
	Factor B	(Varieties)					0.22	
	Factor A × B	(Dates of sowing × varieties)					0.44	
CD	Factor A	(Dates of sowing)					0.51	
P = (0.05)	Factor B	(Varieties)					0.62	
	Factor A × B	(Dates of sowing × varieties)					1.24	

D$_1$= 3rd week of June; D$_2$= 1st week of July; D$_3$= 2nd week of July; D$_4$= 3rd week of July.

Table 5: Morphological traits of various pigeonpea varieties in different sowing dates.

Genotype / Variety	Trichomes on pods (/mm²)									Pod length (mm)	Pod wall thickness (mm)	Seed size (mm)		No. of seeds / pod
	Top			Middle			Lower					Seed length	Seed width	
	A	B	C	A	B	C	A	B	C					
							D₁							
Paras	108.34	5.76	9.17	65.24	4.33	4.2	62.29	0	0.06	52.09	0.83	6.92	4.65	3.3
Manak	110.8	4.82	6.01	75.42	4.14	3.8	81	0.01	0.02	53.24	0.97	6.88	4.42	3.5
AL-201	152.3	8.06	1.68	135.24	6.92	1.87	71.94	0.03	0.02	47.63	2.19	6.72	4.01	2.7
Pusa-992	80.64	2	6	85.84	0.04	5.07	82.31	0.02	0.05	54.12	0.67	7.22	4.56	3.4
PAU-881	105.7	5.78	8.55	97.46	7.98	4	64.38	0	2	49.57	1.67	7.00	4.57	2.9
H03-41	151.46	3.88	8.07	96	6.34	3.8	121.04	1.03	2.93	54.41	1.06	7.26	4.48	4
							D₂							
Paras	107.42	4.18	9.27	55.44	4.39	3.87	59.33	0.07	0.5	49.15	0.71	7.76	4.66	3.68
Manak	116.28	5.34	6.53	86.22	4.04	4	83	0	1.02	40.31	1.39	6.21	4.12	3.31
AL-201	146.78	8.49	1	119.14	7.66	2	83.44	0.8	1	35.62	2.28	6.74	4.58	3.41
Pusa-992	95.12	4.72	6.27	78.31	1.1	5.17	83	0.04	0.5	50.47	1.15	8.22	4.40	3.81
PAU-881	66.32	5.00	8.13	82.66	7.89	6.14	61	0.6	1.87	51.00	1.45	7.56	4.61	4
H03-41	140.33	5.22	7.66	88	6.51	3.78	95.66	0.9	2	50.33	1.44	8.04	4.33	4.06
							D₃							
Paras	113	7.67	8	80.8	4.29	4	60.44	2	1.55	47.44	1.28	7.06	4.55	3.56
Manak	110.06	2.33	6.71	93.07	0.5	4.12	78.34	0.82	0.80	43.17	1.18	6.58	4.39	3.66
AL-201	155.03	6.88	0.88	125.87	6.88	2	80.56	0.61	2.22	37.58	1.88	5.92	4.41	3.3
Pusa-992	78.08	0	7	79.73	1	4.91	67	1.19	0.51	57.29	1.02	8.33	4.68	3.86
PAU-881	79.15	5.778	8.46	88.26	7.69	3.14	70.39	0.07	1.77	44.08	1.76	7.25	4.06	3.51
H03-41	153.73	3.88	7.16	96	6	3.19	109.47	1.46	2.91	45.61	1.83	7.02	4.12	3.79
							D₄							
Paras	110.33	9.22	9.27	78	4	4	62.13	0.1	0	43.00	1.42	5.56	4.44	3.00
Manak	114.8	2.66	6.53	92	1.18	4.36	82.67	0	0.1	48.67	1.28	6.14	4.25	3.26
AL-201	142.1	8.58	1	121.02	9.49	2	84.53	0.09	3	52.42	1.55	7.00	4.76	3.36
Pusa-992	86.91	0.9	6.27	66.44	1.58	4	70.93	1	0	47.35	1.39	6.48	4.45	3.31
PAU-881	67.2	4.46	8.13	85.17	5	4.19	66.66	0.02	0.06	52.71	1.45	7.36	4.86	3.53
H03-41	151.46	6.27	7.64	94	6.59	1.08	118.66	2	3	49.45	1.88	6.76	3.92	2.88

D₁= 3rd week of June; D₂= 1st week of July; D₃= 2nd week of July; D₄= 3rd week of July.

Table 6: Biochemical constituents of pigeonpea varieties in different sowing dates (dry weight basis).

Genotype/ Variety	Pod wall composition on dry weight basis							Green seed composition on dry weight basis						
	TSS (%)	Protein (%)	Phenol (mg g⁻¹)	Chlorophyll (mg g⁻¹)	Moisture (%)	Fat (%)	Tannins (µg g⁻¹)	TSS (%)	Protein (%)	Phenol (mg g⁻¹)	Chlorophyll (mg g⁻¹)	Moisture (%)	Fat (%)	Tannins (µg g⁻¹)
D₁														
Paras	2.68	12.25	0.65	2.41	73.2	2.6	59.80	5.00	23.46	0.75	1.58	73.4	3.3	73.94
Manak	2.69	11.91	0.78	2.26	72.8	2.4	50.54	4.45	24.51	0.42	1.54	71.4	3.3	61.22
AL-201	1.92	10.51	1.92	1.96	69.8	2.9	97.34	2.88	22.76	1.24	1.55	65	4.7	118.87
Pusa-992	2.38	12.25	0.45	2.04	71.6	2.3	34.63	3.04	21.36	0.34	1.43	67	4.0	67.39
PAU-881	2.24	9.46	1.74	1.68	71.2	2	58.03	4.35	21.01	0.68	1.39	67.6	4.2	85.17
H03-41	2.29	11.91	1.99	1.80	69.4	5.2	51.48	4.37	22.10	0.89	1.72	68.2	3.4	94.53
D₂														
Paras	2.01	10.54	1.52	1.59	70.8	2.90	38.71	6.01	21.01	1.35	0.63	64.6	4.8	42.12
Manak	3.26	10.16	1.94	0.98	69.2	1.90	27.16	3.85	21.71	1.14	0.47	62.4	3.5	72.08
AL-201	1.88	10.18	2.97	1.54	70.00	2.00	55.22	5.93	20.31	2.12	0.53	63.2	5.2	81.43
Pusa-992	2.65	10.51	1.21	1.56	69.6	3.00	30.88	4.21	23.46	1.11	0.66	62.2	3.1	29.87
PAU-881	2.50	8.400	2.24	1.47	68.8	3.20	37.44	5.03	19.96	1.63	0.63	68	5.9	53.35
H03-41	2.06	10.86	1.92	1.51	69.2	2.70	33.69	4.54	23.11	1.59	0.29	64.6	4.6	52.41
D₃														
Paras	2.59	11.56	1.68	1.25	68.2	3.2	59.90	4.03	23.41	0.52	0.57	68.6	3.6	37.88
Manak	4.68	10.51	0.69	1.26	69.8	3.3	46.80	5.58	25.56	0.48	0.58	69.2	3.9	45.89
AL-201	1.66	9.11	1.77	0.95	70.4	3.8	117.00	3.35	24.16	0.76	0.71	68	4.6	116.34
Pusa-992	4.10	11.21	0.89	1.03	69	2.5	75.81	4.17	23.46	0.53	0.74	62.2	3.4	90.79
PAU-881	2.37	10.16	1.07	1.03	69	2.9	104.83	4.84	19.96	0.66	0.54	68.6	4.1	121.68
H03-41	3.71	9.81	2.36	1.14	68.6	3.2	63.64	5.87	22.14	0.49	0.74	66.4	3.8	116.06
D₄														
Paras	3.80	12.61	1.59	1.04	72	2.1	34.66	2.74	23.11	1.18	0.95	73.4	3.4	98.28
Manak	6.56	9.11	1.33	1.06	73.4	2.6	73.95	3.96	21.71	0.33	0.93	74	3.6	78.65
AL-201	3.19	9.81	2.69	1.26	70.4	4.3	232.12	2.53	20.31	1.19	0.7	68.6	5.5	239.61
Pusa-992	3.65	12.96	1.46	1.02	70.4	3.3	87.04	1.60	24.16	1.12	0.46	67.4	5.4	136.65
PAU-881	3.43	11.23	1.74	0.81	69.6	4.6	184.39	2.28	25.56	0.98	0.61	68	5.5	120.74
H03-41	2.66	11.68	2.41	1.25	70.4	3.7	82.36	4.08	23.21	0.42	0.58	70.4	4.9	131.97

D_1= 3rd week of June; D_2= 1st week of July; D_3= 2nd week of July; D_4= 3rd week of July.

Effect of elevated CO$_2$ and temperature on resistance resetting

Many studies have observed association between herbivore tolerance and resistance (Bailey and Schweitzer, 2010), but little is known about how abiotic factors like global CO$_2$ and temperature affect the relationship between tolerance and resistance. According to Guo *et al.* (2012) elevated CO$_2$ reduces tomato plant resistance to *H. armigera* by suppressing the critical defensive signal molecule JA and JA-pathway-related defensive enzymes. Tomato plants grown in elevated CO$_2$ are also less tolerant to *H. armigera* than plants grown in ambient CO$_2$. Raised CO$_2$ concentration produce higher leaf glucose concentration and lowered nitrogen content when combined with increased temperature (DeLucia *et al.*, 2012). Both alterations in plant foliage reduce the plant's nutritional value, causing certain herbivores to consume more leaves to meet their nutritional requirement. Srivastava *et al.* (2002) observed the effect of long-term CO$_2$ enrichment on mungbean leaf chemistry. According to the above said researchers, under enriched CO$_2$ (600±50 µl l-1) condition, foliage protein and non-protein nitrogen level decrease whereas, starch and total soluble sugar level of the leaves increase, resulting in more damage by *Spodoptera litura* damage. The change in herbivore feeding behavior caused by enhanced CO$_2$ has led to considerable ecological disruption. Moreover, high CO$_2$ level lowers the titre of plant defense hormone jasmonic acid (JA) and promote the production of salicylic acid (SA), these changes in plant hormones could potentially increase sensitivity to chewing insects (DeLucia *et al.*, 2012).

Not all plant species respond identically to elevated concentrations of CO$_2$ (Lindroth *et al.*, 1993). For example, elevated CO$_2$ results in reduced in foliar nitrogen levels and increased condensed tannin levels in paper birch and but not in white pine (Roth and Lindroth, 1994). Chickpea plants reduce nitrogen-based defensive chemicals (*e.g.*, alkaloids) when CO$_2$ level rose (Sharma *et al.*, 2016b). Reduced resistance in wild tomato plants when grown under high CO$_2$ condition. When wild type tomato plants were infested with *H. armigera* larvae, the levels of jasmonic acid and the activities of lipoxygenase, proteinase inhibitors and polyphenol oxidase were found to be less (Guo *et al.*, 2012) (Fig 1). The expression of resistance and tolerance to the test bug were highest in wild type plants under ambient CO$_2$ level. Increase in susceptibility of soybean plant to Japanese beetle, *Popillia japonica*, by lowering the expression of genes related to the defense hormones (jasmonic acid and ethylene). It decreases the gene expression and activity of cysteine proteinase inhibitors (CystPls), which are the main anti-herbivore defense in plants (Zavala *et al.*, 2010).
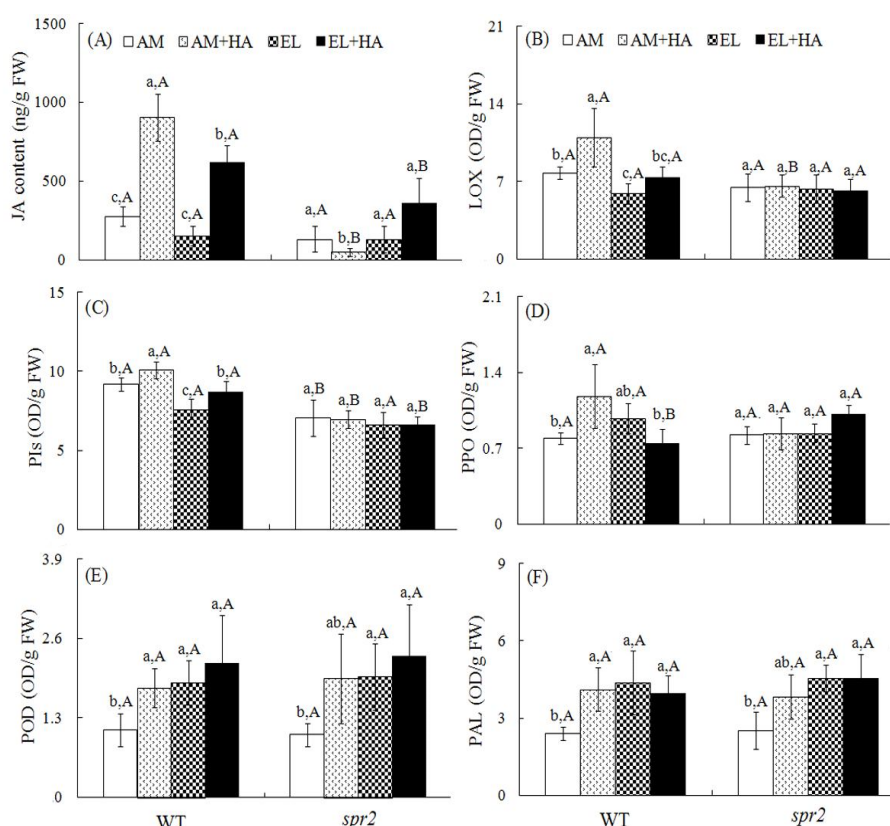

Fig 1: Chemical defensive components in two tomato genotypes grown under ambient (AM) and elevated CO$_2$ (EL) without and with *H. Armigera* (+HA). (A) JA content and the activity of (B) lipoxygenase (LOX), (C) proteinase inhibitors (Pls), (D) polyphenol oxidase (PPO), (E) peroxidase (POD) and (F) phenylalanine ammonia lyase (PAL)

Jasmonic acid lowered the efficiency of soybean plants when CO_2 level were high (Zavala *et al*., 2008). Similarly, increase of CO_2 levels affects the amounts of malic and oxalic acid in chickpea plants, thereby reduce the plant resistance mechanisms against herbivores (Selvaraj *et al*., 2013; Sharma *et al*., 2016b). Plants that grow under elevated levels of CO_2 are more sensitive to the Japanese beetle, *P. japonica* and the western corn rootworm, *D. virgifera* (Zavala *et al*., 2008). The synthesis of cysteine proteinase inhibitors (CystPIs) was reduced due to the down regulation of defense signaling genes (lipoxygenase 7 (lox7), lipoxygenase 8 (lox8) and 1-amino cyclopropane-1-carboxylate synthase (acc-s). These are the principal coleopteran herbivore deterrent chemicals in soybean. On the contrary, when the plants were infested by *P. japonica*, ethylene synthesis in healthy plants increased due to higher CO_2 level but reduced the expression of genes in the ethylene-signaling pathway (Casteel *et al*., 2008).

Pigeonpea plants with the shortest incubation period of 18 hours suffered the most *Phytophthora cajani* infection when grown under 30°C and 85 % RH (Jadesha *et al*., 2019). Similarly, Pande and Sharma (2010) found a higher incidence of phytophthora blight disease when temperature was 28-30°C and relative humidity was between 75 and 96% inferring that. High temperature seems to reduce plant disease resistance, immunity (Dropkin, 1969) and defensive response, making the plant more susceptible to pathogens (Zhu *et al*., 2010).

CONCLUSION

Phytophagous herbivores' interactions with host plants are unquestionably influenced by changing environmental conditions. In general, increased level of CO_2 concentration and temperature interfere with pest–plant interactions. Pest distribution and severity, foliage composition (which determines pest damage) and the physiology and development of foliar feeder herbivores are determined by these parameters. Elevated CO_2 alters C and N-based molecules, phenolic components and tannins present in the plants, reducing their resistance mechanisms. The net result is such that the plants become susceptible to pest on one hand and the insect multiplies beyond the economic threshold level and bring down the legume yield drastically.

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