RESEARCH ARTICLE Legume Research- An International Journal, Volume 49 Issue 4: 673-680 (April 2026)

Effect of Carbon Dioxide Levels on Virulence and Physiological Parameters in Association with Stem Rot Disease of Groundnut

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10.18805/LR-5446

ABSTRACT

Background: Stem rot of groundnut (*Arachis hypogaea* L.) caused by *Scelrotium rolfsii* is the main threat to groundnut production, causing significant economic losses both in India and globally. Despite the economic losses attributed to this pathogen, there are limited reports concerning the virulence and physiological alterations in groundnut in response to increased carbon dioxide levels and pathogen interactions.

Methods: A pot culture experiment was carried out at ICRISAT during the *rabi* season of 2022-23 in Open Top Chambers (OTC) to assess the virulence and physiological parameters of groundnut to climate change and pathogen interactions. The study was carried out at three different carbon dioxide levels (400 ppm, 550 ppm and 700 ppm) using the susceptible cultivar TMV 2 and the moderately resistant cultivar ICGV-14082.

Result: Virulence of the *Sclerotium rolfsii* and physiological responses of groundnut plants were studied. Groundnut plants were grown in open top chambers (OTC) under three different simulated carbon dioxide levels, 400 ppm, 550 ppm and 700 ppm. Virulence of *Sclerotium rolfsii* decreased at increased levels of carbon dioxide levels in both TMV-2 and ICGV-14082 cultivars. Stomatal density and guard cell length in groundnut leaves were decreased as carbon dioxide levels increased.

Key words: Chlorophyll content index, Climate change, Open top chamber (OTC), *Sclerotium rolfsii*, Stomatal density.

INTRODUCTION

Groundnut (*Arachis hypogaea* L.), also known as the “king of oilseeds,” is an annual leguminous crop. It is extensively grown and distributed across more than eighty countries, primarily in tropical and subtropical regions (Madhusudhana, 2013). India ranks as the second-largest producer of groundnut globally, following China. The country plays a significant role in global oilseed production, with a total output of 25.5 million tons from 32.26 million hectares of land (Reddy and Maiti, 2023). In Telangana, groundnut occupies 2.61% of the total cultivated area and 28.18% of the state’s total oilseed acreage. The districts of Mahaboobnagar, Warangal and Nalgonda together account for 86.66% of the groundnut cultivation in the state (Jyothirmai *et al.,* 2019).

The groundnut crop is affected by various diseases caused by fungi, bacteria, nematodes and viruses. These diseases adversely influence both the yield of groundnut pods and the quality of the resulting fodder (Vamshi *et al.,* 2024a). Soil-borne diseases are major constraints in groundnut production. *S. rolfsii* is a soil-borne plant pathogen inciting root rot, stem rot, collar rot, wilt and foot rot diseases in over 500 plant species of agricultural and horticultural crops worldwide (Vamshi *et al.,* 2025). Stem rot also known as Sclerotium blight, Sclerotium rot, southern blight, southern stem rot, Sclerotium wilt, root rot, pod rot and white mold caused by *Sclerotium rolfsii* Sacc (Babu and Deepika, 2022). The development and survival of *S. rolfsii* are favored by high temperatures and moisture. The disease typically manifests in crops around one month of age, where the fungal mycelium covers the stem near the soil surface. This mycelium releases organic acids that damage plant cells and cause necrosis. The key symptoms of the disease include the presence of mycelium and sclerotia on the affected tissues (Kumar *et al.,* 2008). According to Akgul *et al.* (2011), stem rot results in crop losses of 27% in India, 10-50% in South America and over 25% in Australia, with losses in heavily infected fields potentially reaching as high as 80% (Yan *et al.,* 2019; Mayee

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How to cite this article: Vamshi, J., Devi, G.U., Gireesha, D., Navyashree, R., Belagalla, N., Hanamasagar, Y. and Sudini, H.K. (2026). Effect of Carbon Dioxide Levels on Virulence and Physiological Parameters in Association with Stem Rot Disease of Groundnut. *Legume Research.* **49(4):** 673-680. doi: 10.18805/LR-5446.

Submitted: 11-11-2024 **Accepted:** 06-03-2025 **Online:** 04-04-2025

and Datar, 1988). The disease is most prevalent during the kharif season, often occurring alone or in conjunction with other diseases and it can lead to substantial yield reductions. Stem rot is considered one of the most destructive and widespread diseases affecting groundnut crops, especially in the northwestern plain region of Rajasthan (Sharma *et al.,* 2012).

Air is a crucial resource for the survival and growth of living organisms. The composition of trace elements in the air can fluctuate due to emissions from various industrial and urban activities (Chen *et al.,* 2017). In developing nations, fossil fuels remain the primary energy source for industrial operations, leading to the release of significant amounts of CO_2. This has contributed to an increase of approximately 28% in the atmospheric CO_2 concentration, which has risen from over 400 ppm (parts per million) today, compared to 311 ppm in the mid-nineteenth century (NASA GISS). Globally climate change is expected to pull down groundnut productivity by 11-25% (Sudhalakshmi *et al.,* 2022). If the current pattern of fossil fuel consumption and population growth persists, CO_2 levels in the atmosphere could reach 500-1000 ppm by the year 2100 (IPCC 2013). Such elevated CO_2 concentrations could affect plant growth and the interactions between plants and pathogens (Khan and Khan, 2000). Although carbon dioxide is not toxic to plants, it can stimulate plant growth and increase biomass production (Dader *et al.,* 2016). This growth stimulation occurs due to a higher rate of CO_2 fixation, which reduces photorespiration (Li *et al.,* 2007). The enhanced rate of photosynthesis under higher CO_2 levels typically results in increased plant growth and biomass. The extent of this growth promotion varies depending on the plant type: C3 plants (which make up the majority of plant species) experience a 30-34% increase in growth, while C4 plants (such as grasses in the Poaceae family) show a 10-15% increase (Kimball, 1983; Prior *et al.,* 2003). Additionally, elevated CO_2 can affect other physiological and biochemical processes in plants (Agarwal and Deepak, 2003; Jiang *et al.,* 2012). For example, higher CO_2 concentrations negatively impact stomatal conductance and transpiration rates (Ainsworth and Rogers, 2007). Furthermore, increased CO_2 levels (500-600 ppm) promote the production of chlorophyll and other leaf pigments (Sun *et al.,* 2015).

In this regard, the current study seeks to assess the virulence of *Sclerotium rolfsii* and the physiological responses of plants when exposed to elevated CO_2 concentrations of 400 ppm, 550 ppm and 700 ppm.

MATERIALS AND METHODS

Treatment setup in open top chambers (OTC)

A pot culture experiment was conducted at ICRISAT during the *rabi* season of 2022-23 in open top chambers (OTC) to evaluate the virulence and physiological responses of groundnut to climate change and pathogen interactions. The study was performed at three different carbon dioxide concentrations (400 ppm, 550 ppm and 700 ppm) using the susceptible cultivar TMV 2 and the moderately resistant cultivar ICGV-14082. Seedlings that were 30-35 days old were inoculated by applying the pathogen inoculum to the subsurface of the soil. Observations were made on the incubation period (IP), days to permanent wilting (DPW), disease incidence, disease severity and mortality.

Disease severity assessments were made by using a 1-5 disease severity scale (Shokes *et al.,* 1996). Where,

Severity scale	Description
1	A healthy plant.
2	Lesions on stems only.
3	Up to 25% of the plant symptomatic (wilted, dying or dead).
4	26-50% of the plant symptomatic.
5	>50% of the plant symptomatic.

The per cent disease severity was calculated using the formula (Le *et al.,* 2012):

$$\text{Disease severity (\%)} = \frac{\sum ab}{AK} \times 100$$

Where,

a = Number of diseased plants having the same degree of infection.

b = Degree of infection.

A = Total number of plants examined.

K = Highest degree of infection.

Estimation of physiological changes occurring in groundnut in response to climate change and pathogen interaction

Stomatal density and guard cell length

Suitable leaves were collected from groundnut seedlings at 0, 2, 4, 6, 8 and 10 days post-inoculation, grown in OTC chambers. The leaves were gently washed with running water to remove dust and debris, then allowed to air dry. A replica fluid, such as Quick Fix, was applied in a thin, even layer by placing a drop or two on the leaf surface and allowing it to dry completely. Once dry, the replica was carefully peeled off using forceps or fingers and placed onto a slide, then covered with a cover slip. The number of stomata in the microscopic field was counted to calculate the stomatal density, which was expressed as stomata per mm^2. Stomatal density and guard cell length were measured using Image-J software in the leaves of groundnut plants inoculated with the virulent *S. rolfsii* isolate (SrPWp) in OTC chambers at 2-day intervals.

Chlorophyll content index (CCI)

A portable, non-invasive and lightweight device (SPAD-502 chlorophyll meter, Konica-Minolta, Japan) was used to measure the Chlorophyll Content Index (CCI). Fully mature leaves were selected at 0, 2, 4, 6, 8 and 10 days post-inoculation from groundnut seedlings grown in OTC chambers. Three CCI readings were taken from each pot

and the average value was calculated to determine the mean CCI for each pot.

Statistical analysis

Per cent data was converted into arc sin values and square root transformed values. Fischer's method of analysis of variance was used for analysis and interpretation of the data (Gomez and Gomez, 1984). Other statistical analysis *viz*., OP STAT online statistical analysis program developed by Hissar Agricultural University, IBM SPSS and MS-excel were used to analyze the data.

RESULTS AND DISCUSSION

The potential impact of climate change on plant-pathogen interactions and its effect on crop production is a topic of considerable debate. It presents a significant challenge for future programs aimed at managing diseases in the context of global environmental changes.

The results (Table 1) showed that the incubation period of the pathogen lengthened as CO_2 concentrations increased from 400 to 700 ppm in both the susceptible cultivar TMV-2 and the moderately resistant cultivar ICGV-14082. However, no change was observed in the days to permanent wilting in the moderately resistant cultivar, which remained greater than 32 across all three CO_2 levels. In contrast, in the susceptible cultivar, the days to permanent wilting increased from 6.42 at 400 ppm to 13.90 at 550 ppm and further to 16.58 at 700 ppm.

In the TMV-2 cultivar, exposure to 700 ppm of CO_2 resulted in the highest mean incubation period (IP) of 8.25 (Table 1) (Fig 1), the longest days to permanent wilting (DPW) of 16.58 (Table 1) and the lowest disease incidence (90.22) (Table 2), disease severity (88.36) (Table 3) and mortality (82.82) (Table 4) (Fig 1). These values were similar to those observed at 550 ppm CO_2, which showed a mean IP of 6.92, DPW of 13.90, disease incidence of 94.82, disease severity of 91.00and mortality of 86.17. In contrast, at 400 ppm CO_2, the lowest mean IP (5.33), DPW (6.42)and the highest disease incidence (100.00), disease severity (100.00) and mortality (100.00) were recorded. These findings suggest that the virulence of *S. rolfsii* decreased as CO_2 levels increased in the TMV-2 cultivar.

In the ICGV-14082 cultivar, exposure to 700 ppm of CO_2 resulted in the highest mean incubation period (IP) of 16.90 (Table 1), the longest days to permanent wilting (DPW) (>32) (Table 1) and the lowest disease incidence (42.52) (Table 2), disease severity (40.18) (Table 3) and mortality (14.50) (Table 4) (Fig 1). These values were

Table 1: Effect of CO_2 on incubation period (IP) and days to permanent wilting (DPW) of *Sclerotium rolfsii* of groundnut cultivars (TMV-2) and (ICGV 14082) under open top chambers (OTC).

CO_2 levels	Incubation period (IP)		Days to permanent wilting	
	TMV-2	ICGV 14082	TMV-2	ICGV 14082
400 ppm	5.33	11.25	6.42	>32
550 ppm	6.92	13.80	13.90	>32
700 ppm	8.25	16.90	16.58	>32
Control	0.00	0.00	0.00	0.00

Factors	IP			DPW		
	CD (0.01)	S.Em.±	CV (%)	CD (0.01)	S.Em.±	CV (%)
CO_2 levels	0.28	0.09	2.40	1.07	0.35	5.70
Variety's	0.40	0.13		1.52	0.52	
Interaction	0.57	0.19		2.15	0.71	

Table 2: Effect of CO_2 on disease incidence of *Sclerotium rolfsii* of groundnut cultivars (TMV-2) and (ICGV 14082) under open top chambers (OTC).

CO_2 levels	15 DPI*		30 DPI		Mean	
	TMV-2	ICGV-14082	TMV-2	ICGV-14082	TMV-2	ICGV-14082
400 ppm	100.00 (90.00)**	48.26 (44.00)	100.00 (90.00)	52.48 (46.42)	100.00 (90.00)	50.37 (45.21)
550 ppm	93.45 (75.27)	45.34 (42.32)	96.20 (78.95)	48.20 (43.97)	94.82 (77.11)	46.77 (43.14)
700 ppm	88.64 (70.41)	41.37 (40.03)	91.81 (73.49)	43.68 (41.36)	90.22 (71.95)	42.52 (40.69)
Control	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)

Factors	15 DPI			30 DPI		
	CD (0.01)	S.Em.±	CV (%)	CD (0.01)	S.Em.±	CV (%)
CO_2 levels	3.75	1.25	6.52	1.83	0.61	4.51
Variety's	5.30	1.77		2.58	0.86	
Interaction	7.50	2.50		3.66	1.22	

*dpi - Days post inoculation; **Figures in the parenthesis are arc sine transformed values.

similar to those observed at 550 ppm CO_2, which showed a mean IP of 13.80, DPW (>32), disease incidence of 46.77, disease severity of 46.01and mortality of 18.35. In contrast, at 400 ppm CO_2, the lowest mean IP (11.25) and the highest disease incidence (50.37), disease severity (49.79) and mortality (21.20) were recorded, while the DPW remained >32. These results suggest that the virulence of *S. rolfsii* decreased as CO_2 levels increased in the ICGV-14082 cultivar.

The disease incidence was reduced by 49.63% in the moderately resistant cultivar ICGV-14082 compared to the susceptible cultivar TMV-2 at 400 ppm CO_2. A similar pattern was observed at 550 ppm (48.05%) and 700 ppm (47.7%).

Disease severity decreased by 50.21% in ICGV-14082 relative to TMV-2 at 400 ppm CO_2, with a similar trend at 550 ppm (44.99%) and 700 ppm (48.18%).

Mortality was lower by 78.8% in ICGV-14082 compared to TMV-2 at 400 ppm CO_2 and this trend continued at 550 ppm (67.82%) and 700 ppm (68.32%).

Our results align with those of Griffin and Nair (1968), who found that the growth rate of *Sclerotium rolfsii* mycelium remained constant within oxygen concentrations ranging from 3% to 21%, but decreased progressively as the carbon dioxide concentration rose above approximately 0.03%. Similarly, Kritzman and Henis (1977) reported that the growth rate and sclerotial production of *S. rolfsii* were significantly inhibited at a CO_2 concentration of 10%. In the same vein, Imolehin and Grogan (1980) observed that there were no significant differences in radial growth and sclerotial production when oxygen concentrations ranged from 4% to 21% (normal air) and CO_2 levels were at 0.03%. However, when the oxygen concentration dropped below 4% and CO_2 exceeded 8%, both radial growth and sclerotial production were greatly reduced. Furthermore, Punja and Jenkin (1984) reported that sclerotial germination was completely inhibited at temperatures between 9-12°C, at water potentials lower than -60 bars and under conditions of CO_2 and O_2 levels exceeding 20% and dropping below 3%, respectively.

Physiological changes

Chlorophyll content index (CCI)

Chlorophyll content index (CCI) was measured using a SPAD meter in the leaves of groundnut plants inoculated

Table 3: Effect of CO_2 on disease severity of *Sclerotium rolfsii* of groundnut cultivars (TMV-2) and (ICGV 14082) under open top chambers (OTC).

CO_2 levels	15 DPI*		30 DPI		Mean	
	TMV-2	ICGV-14082	TMV-2	ICGV-14082	TMV-2	ICGV-14082
400 ppm	100.00 (90.00)**	45.37 (42.34)	100.00 (90.00)	54.22 (47.43)	100.00 (90.00)	49.79 (44.88)
550 ppm	88.23 (70.07)	42.28 (40.55)	93.78 (75.78)	49.75 (44.86)	91.00 (72.92)	46.01 (42.70)
700 ppm	86.48 (68.43)	35.92 (36.82)	90.25 (71.99)	44.44 (41.81)	88.36 (70.21)	40.18 (39.31)
Control	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Factors	15 DPI			30 DPI		
	CD (0.01)	S.Em.±	CV (%)	CD (0.01)	S.Em.±	CV (%)
CO_2 levels	1.80	0.60	4.78	1.99	0.66	4.96
Variety's	2.55	0.85		2.82	0.94	
Interaction	3.60	1.20		3.99	1.33	

*dpi- Days post inoculation.

**Figures in the parenthesis are arc sine transformed values.

Table 4: Effect of CO_2 on mortality of *Sclerotium rolfsii* of groundnut cultivars (TMV 2) and (ICGV 14082) under open top chambers (OTC).

CO_2 levels	15 DPI*		30 DPI		Mean	
	TMV-2	ICGV-14082	TMV-2	ICGV-14082	TMV-2	ICGV-14082
400 ppm	100.00(90.00)**	17.74(24.90)	100.00(90.00)	24.67(29.78)	100.00(90.00)	21.20(27.34)
550 ppm	83.87(66.45)	14.38(22.28)	88.48(70.18)	22.33(28.19)	86.17(68.31)	18.35(25.24)
700 ppm	80.35(63.78)	10.48(18.86)	85.30(67.47)	18.52(25.48)	82.82(65.62)	14.50(22.17)
Control	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)
Factors	15 DPI			30 DPI		
	CD (0.01)	S.Em.±	CV (%)	CD (0.01)	S.Em.±	CV (%)
CO_2 levels	0.73	0.24	2.38	1.01	0.33	3.02
Variety's	1.04	0.34		1.43	0.48	
Interaction	1.47	0.49		2.03	0.67	

*dpi- Days post inoculation.

**Figures in the parenthesis are arc sine transformed values.

with the virulent *S. rolfsii* isolate (SrPWp) in the OTC chamber at two-day intervals (Fig 2).

In the TMV-2 cultivar, the highest average CCI of 33.23 µmol m^2 was recorded at 700 ppm of carbon dioxide, followed by 33.08 µmol m^2 at 550 ppm and 30.76 µmol m^2 at 400 ppm.

In the ICGV-14082 cultivar, the highest average CCI of 40.91 µmol m^2 was recorded at 700 ppm, followed by 39.96 µmol m^2 at 550 ppm and 34.41 µmol m^2 at 400 ppm.

The CCI was 11.86% higher in the infected ICGV-14082 cultivar compared to the infected TMV-2 cultivar at 400 ppm CO_2, with increases of 20.79% at 550 ppm and 23.11% at 700 ppm.

These results indicate that the chlorophyll content index increased as carbon dioxide concentrations rise.

Our findings are consistent with those of Habash *et al.* (1995), who demonstrated that wheat grown under elevated CO_2 conditions exhibited higher levels of chlorophyll pigments. Similarly, De Costa *et al.* (2003) reported that elevated CO_2 concentrations enhanced leaf chlorophyll content in rice. Furthermore, Haque *et al.* (2006) investigated the impact of elevated CO_2 (570±50 µmol mol^{-1})

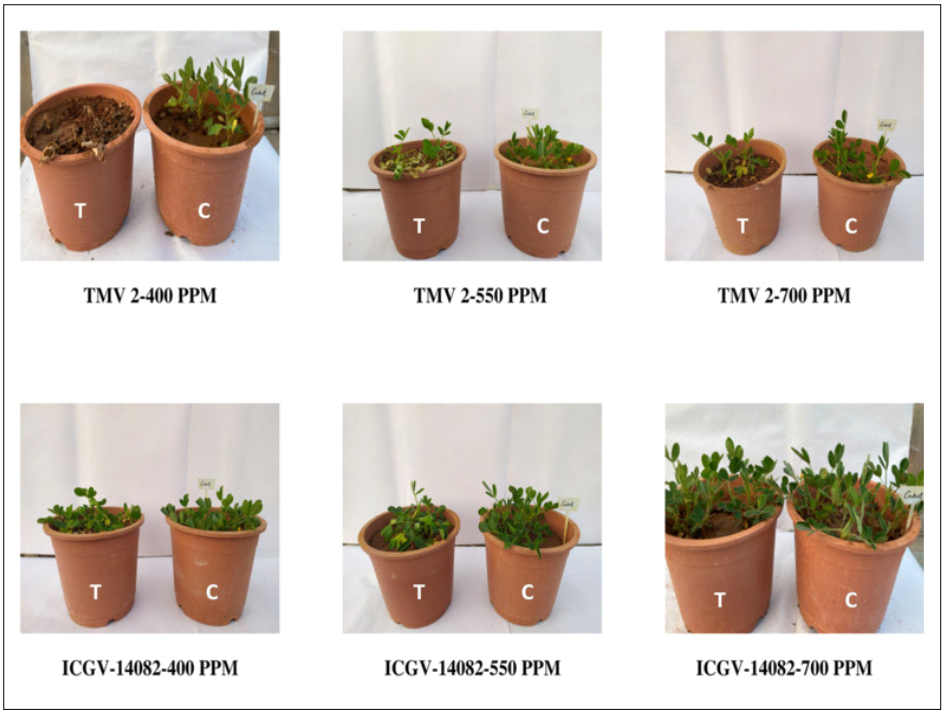


Fig 1: Effect of CO_2 levels on susceptible cultivar (TMV 2) and moderately resistant cultivar (ICGV-14082) with virulent isolate of *Sclerotium rolfsii.*

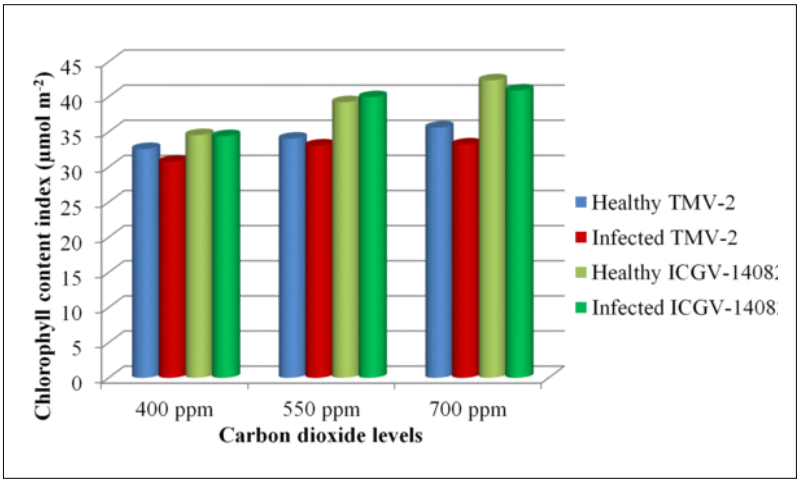


Fig 2: Effect of carbon dioxide levels on chlorophyll content index (CCI) (µmol m^{-2}) in susceptible cultivar (TMV 2) and moderately resistant cultivar (ICGV-14082) groundnut plants.

on leaf chlorophyll (Chl), nitrogen (N) content and photosynthetic rate (PN) during the post-flowering phase of rice grown in an Open Top Chamber (OTC). They found that both Chl and N contents were highest at the time of flowering under elevated CO_2 conditions, compared to ambient CO_2 levels (~365 µmol mol^{-1}) in OTC and open field conditions.

Stomatal density

Stomatal density was measured using Image-J software in the leaves of groundnut plants inoculated with the virulent *S. rolfsii* isolate (SrPWp) in an OTC chamber at two-day intervals (Fig 3).

In the TMV-2 cultivar, the highest average stomatal density of 217.1 stomata mm^{-2} was recorded at 400 ppm of CO_2, followed by 204.3 stomata mm^{-2} at 550 ppm and 200.6 stomata mm^{-2} at 700 ppm.

In the ICGV-14082 cultivar, the highest average stomatal density of 207.5 stomata mm^{-2} was recorded at 400 ppm, followed by 194.0 stomata mm^{-2} at 550 ppm and 189.9 stomata mm^{-2} at 700 ppm.

The stomatal density was 4.62% lower in the infected ICGV-14082 cultivar compared to the infected TMV-2 cultivar at 400 ppm CO_2, with reductions of 5.30% at 550 ppm and 5.63% at 700 ppm. These results indicate that stomatal density decreased as CO_2 concentrations increased.

Our findings are consistent with those of Clifford *et al.* (1995), who observed that when groundnut plants were grown under irrigated conditions with unrestricted root systems, an increase in atmospheric CO_2 from 375 to 700 ppm reduced stomatal frequency on both leaf surfaces by up to 16%. Similarly, Gitz *et al.* (2017) reported that elevated CO_2 levels led to a reduction in both the initiation of

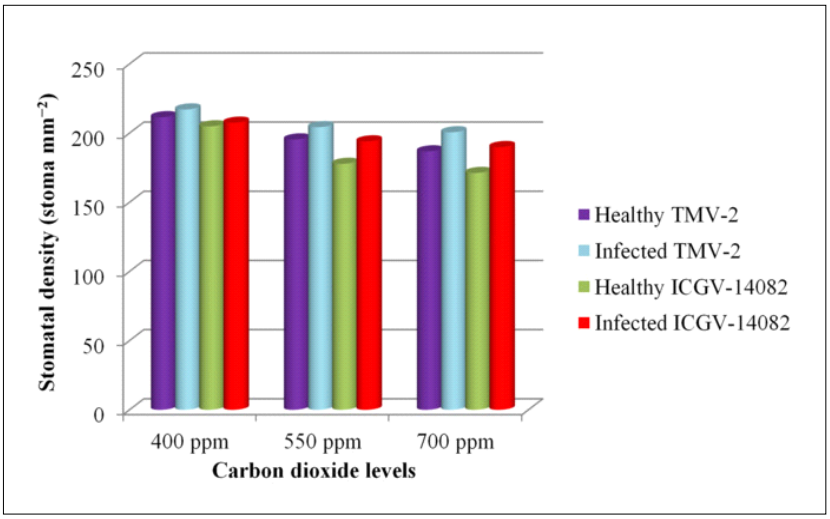


Fig 3: Effect of carbon dioxide levels onstomatal density (stoma mm^{-2}) in susceptible cultivar (TMV 2) and moderately resistant cultivar (ICGV-14082) groundnut plants.

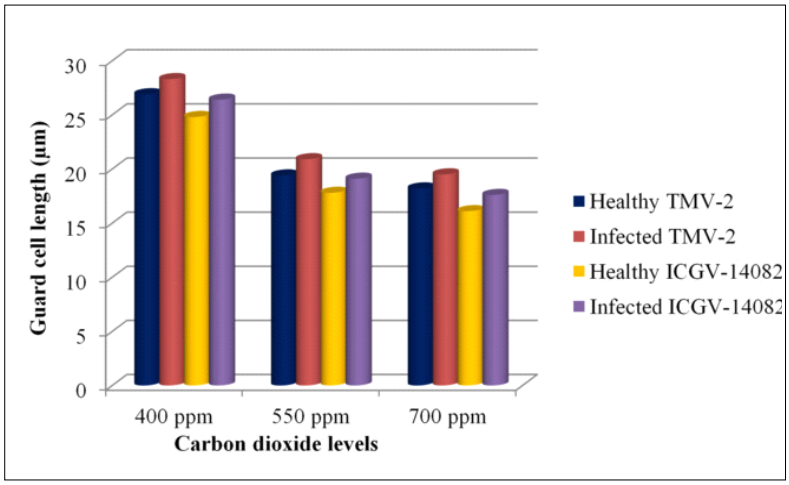


Fig 4: Effect of carbon dioxide levels on guard cell length (µm) in susceptible cultivar (TMV 2) and moderately resistant cultivar (ICGV-14082) groundnut plants.

stomatal development on the adaxial and abaxial surfaces, as well as a decrease in stomatal density and size.

Guard cell length

Guard cell length was measured using Image-J software in the leaves of groundnut plants inoculated with the virulent *S. rolfsii* isolate (SrPWp) in an OTC chamber at two-day intervals (Fig 4).

In the TMV-2 cultivar, the highest average guard cell length of 28.3 µm was recorded at 400 ppm of CO_2, followed by 20.9 µm at 550 ppm and 19.5 µm at 700 ppm.

In the ICGV-14082 cultivar, the highest average guard cell length of 26.4 µm was recorded at 400 ppm, followed by 19.1 µm at 550 ppm and 17.6 µm at 700 ppm.

The guard cell length was 7.19% shorter in the infected ICGV-14082 cultivar compared to the infected TMV-2 cultivar at 400 ppm CO_2, with reductions of 9.42% at 550 ppm and 10.79% at 700 ppm. These results suggest that guard cell length decreased as CO_2 levels increased.

Our findings are consistent with those of Gitz *et al.* (2017), who reported that elevated CO_2 led to a decrease in both the initiation of stomatal development on the adaxial and abaxial surfaces, as well as a reduction in stomatal density and size.

CONCLUSION

The virulence of *Sclerotium rolfsii* was reduced at higher carbon dioxide concentrations in both the TMV-2 and ICGV-14082 cultivars. As carbon dioxide levels increased, the chlorophyll content index in groundnut leaves also showed an increase. However, stomatal density and guard cell length in the leaves decreased with rising CO_2 levels. Since *Sclerotium rolfsii* is an oxygen-dependent pathogen, its virulence diminished as carbon dioxide concentrations increased.

Conflict of interest

The authors declare that they have no conflict of interest.

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