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Evaluating the combined effects of elevated ozone and carbon dioxide on seed-related traits in Indian mustard (*Brassica juncea)*

GAYATHRI JAWAHARJOTHI[1], D K SHARMA[1*], ARTI BHATIA[1], MANJUNATH PRASAD[1],
BOOMIRAJ KOVILPILLAI[2], SUDHIR KUMAR[1] and VIJAY DUNNA[1]

ICAR-Indian Agricultural Research Institute, New Delhi 110 012, India

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ABSTRACT

An experiment was conducted during winter (*rabi*) seasons 2020–21 and 2021–22 at ICAR-Indian Agricultural Research Institute, New Delhi, aimed to evaluate the influence of elevated conditions on seed germination in Indian mustard. Three winter Indian mustard (*Brassica juncea)* varieties (PDZM 31, Pusa Bold, and PM 30) to study the effects of elevated ozone (65 ± 10 ppb), elevated carbon dioxide (550 ± 10 ppm), and their interaction under FAOE, FACE, and FAOCE treatments. The impact of elevated ozone, carbon dioxide, and their interaction on seed-related traits remains scarce and underexplored. The results showed that seed germination traits (germination percentage, speed of germination, uniformity in germination, seedling shoot length, and seedling shoot width) and seed size parameters (seed length and seed width) were negatively affected by elevated ozone at different growth stages of Indian mustard. Additionally, significant changes were observed under elevated CO_2. Notably, under interaction treatments, elevated CO_2 was found to mitigate the detrimental effects of elevated ozone, providing insights into potential adaptation strategies for mustard cultivation under future climatic conditions.

Keywords: Elevated ozone, Elevated CO_2, Seed germination, Speed of germination, Uniformity in germination

Tropospheric ozone is a harmful air pollutant formed by chemical reactions involving nitrogen oxides and volatile organic compounds in the presence of sunlight. Across the globe, ozone levels may reach 60–70 ppb by 2100 (Pachauri *et al.* 2014), significantly affecting plant physiology. Similarly, atmospheric CO_2 levels are projected to reach 540–970 ppm by 2100 (Pachauri and Reisinger 2007). Elevated CO_2 enhances C_3 plant photosynthesis, but trade-offs include reduced micronutrient content (Ebi and Loladze 2019).

The atmospheric CO_2 concentrations have increased at least by 35%, and are forecasted to reach 700 ppm (NOAA 2019) and 540–970 ppm by the year 2100 (Pachauri and Reisinger 2007). Increased levels of carbon dioxide (CO_2) increased the photosynthesis of C_3 plants (wheat, rice, potatoes and barley) by enhancing agricultural yields however, those yield gains come at the expense of reduced nutritional quality as plants collect more carbohydrates and fewer micronutrients (such as iron and zinc), which might have a detrimental impact on human nutrition (Ebi and Loladze 2019). FACE (Free Air Ozone Enrichment) experiments offer crucial information on future CO_2 and O_3 impacts on ecosystems and emphasise the significant interacting effects of temperature, nutrients, and water supply in influencing ecosystem responses to air pollution (Ainsworth *et al.* 2019).

Mustard ranks third among global oilseed crops, covering 24.7% of India's oilseed-growing area (MoAFW 2019). Elevated ozone levels adversely affect crop photosynthesis and gas exchange parameters, damaging leaf tissues (Daripa *et al.* 2016). However, studies on ozone and CO_2 interactions affecting mustard seed traits remain scarce. Therefore, this study investigates how elevated ozone and CO_2 influence seed germination and seedling traits in double-zero, conventional and single-zero Indian mustard (*Brassica juncea)* varieties.

MATERIALS AND METHODS

An experiment was conducted during winter (*rabi*) seasons 2020–21 and 2021–22 at ICAR-Indian Agricultural Research Institute, New Delhi. The soil type was Typic Haplustept, belonging to Indo-Gangetic alluvium, non-calcareous, and slightly alkaline (Kumar *et al.* 2021). Three mustard varieties were tested under: FAOE (Free Air Ozone Enrichment: 65 ± 10 ppb O_3), FACE (Free Air

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[1]ICAR-Indian Agricultural Research Institute, New Delhi; [2]Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu. *Corresponding author email: dineshpusa69@gmail.com

Carbon Dioxide Enrichment: 550 ± 10 ppm CO_2); FAOCE (Combined O_3 and CO_2 enrichment).

Each plot size was 3 m × 3 m and a horizontal perforated tubing was used to disperse gases, ensuring uniform exposure. The elevated ozone was generated by using Ozone generator and CO_2 gases were fumigated from the CO_2 tank. The harvested seeds from the exposed plant throughout the season were used for observation. The detailed experimental details are given in Jawaharjothi *et al.* 2023.

Seed germination: A uniform-sized germination plate with Whatman filter paper in which germination was initiated by dispensing demineralized water to each petriplate. The randomly selected 50 seeds/treatment with 4 replications were spread onto filter paper, distributed equally in the petri plates, and the plates were placed in an incubator or climate chamber maintained at 20°C. Seeds were considered germinated, if the radicle protruded by at least 2 mm. The observations were carried out at different intervals, where the determination of seed germination percentage, speed of germination, and uniformity in germination. The seedling's shoot length and root length were measured after 8 days. Germination parameters, namely, total seed germination on the 5th day (G_{max}, in percentage) and time for 50% germination (t_{50}, in hrs), were calculated by automatically scoring the germination over time with GERMINATOR software (Joosen *et al.* 2010).

Seed size: The seed size was determined by using SMARTGRAIN software (Tanabata *et al.* 2012). 1 g of seeds was evenly distributed and scanned. The scanned image was uploaded into the software to analyse the seed length (L) and seed width (W).

Statistical analysis: An Analysis of variance (ANOVA) was done using a completely randomized design to check whether the treatment differences were statistically significant using Web Agri Stat Package 2.0 (WASP 2.0) developed by ICAR-Central Coastal Agricultural Research Institute (Jangam and Wadekar 2004) and also by GraphPad Prism 9.3.1 version statistical tool.

RESULTS AND DISCUSSION

Changes in total seed germination (%) under different treatments: Elevated ozone significantly reduced seed germination across all varieties (P≤0.0001). The highest germination reduction was observed in Pusa Bold (92.25%), followed by PDZM 31 and PM 30 (94.25%). The interaction between treatment and genotype in total seed germination percentage was significant at P≤0.05. Under elevated ozone conditions, the seed germination rate declined in the order of Pusa Bold (92.25%) < PDZM 31 and PM 30 (94.25%), followed by a reduction in seed germination in Pusa Bold (98.25%) < PM 30 (98.5%) < PDZM 31 (99.25%). In contrast, ambient and elevated CO_2 treatments across all genotypes recorded the highest germination rate of 100%, as illustrated in Fig. 1. Our findings align with those of Violleau *et al.* (2008), who reported that prolonged exposure to high ozone concentrations significantly impacted seed germination, whereas short-term exposure at lower concentrations had beneficial effects. Similarly, Abeli *et al.* (2017) demonstrated that ozone exposure at 185 ppb for five days delayed germination and reduced germination percentage in alpine plants, whereas exposure at 125 ppb for 5–10 days resulted in improved germination rates.

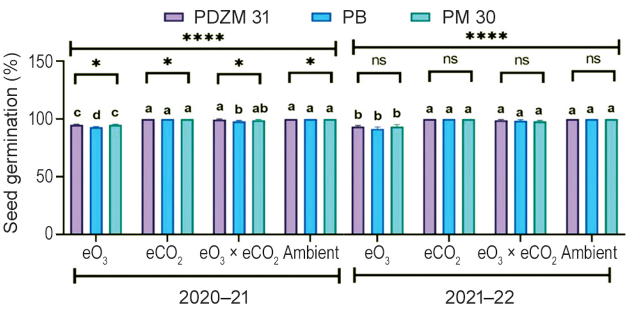

Fig. 1 Impacts of elevated ozone, carbon dioxide and their interaction on total seed germination percentage in different Indian mustard genotypes (PDZM 31, PB and PM 30) for two seasons.

Changes in speed of germination (t_{50} in hours) under different treatments: The speed of germination (t_{50} in hrs) under different treatments (elevated O_3, CO_2, O_3 × CO_2, and ambient conditions) in Indian mustard genotypes (PDZM 31, Pusa Bold, and PM 30) showed significant variation (P≤0.0001) across both seasons. However, the interaction between treatments and genotypes was found to be non-significant. In the first season, the highest speed of germination was observed in PDZM 31 (33.7 hrs) and PM 30 (33.5 hrs) under elevated ozone conditions, followed by Pusa Bold (32.9 hrs) > PDZM 31 (32 hrs), PM 30 (32 hrs), and Pusa Bold (31.8 hrs). The lowest speed of germination was recorded in all genotypes under ambient conditions, followed by the carbon dioxide treatment (30.6 hrs). Similar trends were observed in the second season, as illustrated in Fig. 2. The 1.5% decline in germination speed under elevated ozone may be attributed to the triggering of antioxidants such as abscisic acid, which regulates hormone levels, breaks dormancy, and influences germination (Dong *et al.* 2022). According to Hampton *et al.* (2013) and Zhang *et al.* (2020),

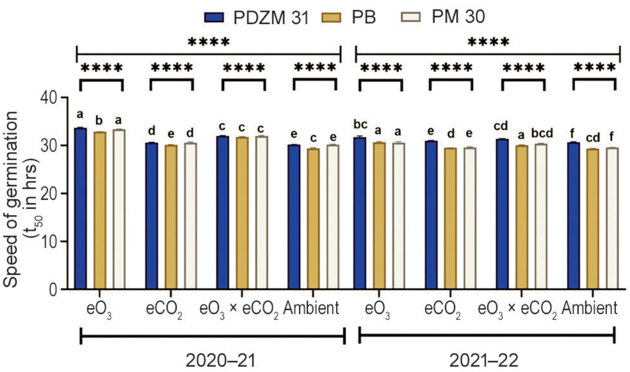

Fig. 2 Impacts of elevated ozone, carbon dioxide and their interaction on the speed of germination (t_{50} in hours) in different Indian mustard genotypes (PDZM 31, PB and PM 30) for two seasons.

seed nitrogen (N) concentration has a significant impact on early germination and subsequent seedling development. Furthermore, a strong association between seed N, seed germination, and seed vigour was observed, suggesting that a decrease in seed protein content caused by elevated CO_2 (eCO_2) may negatively impact germination and vigour (Lamichaney *et al.* 2021).

Changes in uniformity of germination (U9010 in hrs) under different treatments: The elevated levels (O_3, CO_2, $O_3 \times CO_2$, and ambient) in Indian mustard showed significant differences among treatments ($P \leq 0.0001$ in 2020–21 and $P \leq 0.01$ in 2021–22) and genotypes ($P \leq 0.0001$ in 2020–21 and $P \leq 0.001$ in 2021–22). The time taken for seeds to achieve germination from 10–90% was recorded, with the longest germination times observed under elevated O_3 (10.73 h in Pusa Bold > 9.12 hrs in PM 30 > 8.53 hrs in PDZM 31). This was followed by the interaction treatment (10.37 hrs in Pusa Bold > 8.24 hrs in PM 30 > 7.54 hrs in PDZM 31). The most uniform germination time was recorded under ambient conditions (3.37 hrs in PDZM 31 > 3.56 hrs in PM 30 > 7.43 hrs in Pusa Bold) and elevated CO_2 conditions (5.31 hrs in PDZM 31 > 5.37 hrs in PM 30 > 7.37 hrs in Pusa Bold). Similarly, in the second season, the highest uniformity was observed under elevated CO_2 and ambient conditions, whereas the lowest uniformity was recorded under $O_3 \times CO_2$ interactions and ozone treatments (Fig. 3). According to Rajjou *et al.* (2012), proteins in the seed embryo and endosperm play a crucial role in cell proliferation, expansion, and seedling development, which are essential for seed germination. Previous studies indicate that low-vigour seeds exhibit slower protein degradation (Sekar *et al.* 2015). Likely, the decline in protein content under high CO_2 levels did not surpass the threshold required to significantly impact germination. Given the flexibility in endosperm enzyme expression related to protein degradation, the nitrogen or protein content in seeds varies significantly depending on genotype and environmental conditions (Holman *et al.* 2009, Zhao *et al.* 2009).

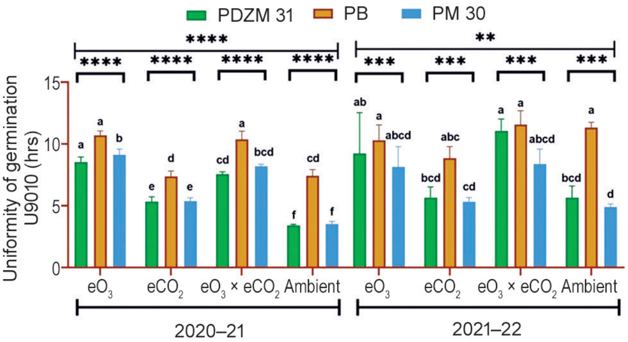

Fig. 3 Impacts of elevated ozone, carbon dioxide and their interaction on uniformity in germination (U9010 in hours) in different Indian mustard genotypes (PDZM 31, PB and PM 30) for two seasons.

Changes in seed length and seed width under different treatments: The seed size (seed length and seed width) showed significant variations among treatments ($P \leq 0.001$),

Table 1 Effect of eO_3, eCO_2, $eO_3 \times eCO_2$ and ambient on seed length and seed width of different genotypes

		Seed length (mm)		Seed width (mm)	
Treatments	Genotypes	2020–21	2021–22	2020–21	2021–22
eO_3	PDZM 31	2.35 ± 0.03^{bc}	2.07 ± 0.02^{f}	2.16 ± 0.03^{b}	1.78 ± 0.02^{c}
	Pusa Bold	2.26 ± 0.01^{cd}	2.12 ± 0.04^{def}	1.71 ± 0.04^{e}	1.61 ± 0.04^{e}
	PM 30	1.85 ± 0.02^{e}	2.03 ± 0.06^{f}	1.40 ± 0.01^{g}	1.51 ± 0.03^{f}
eCO_2	PDZM 31	2.62 ± 0.01^{a}	2.27 ± 0.01^{bc}	2.37 ± 0.01^{a}	1.99 ± 0.01^{b}
	Pusa Bold	2.38 ± 0.02^{bc}	2.26 ± 0.02^{bc}	1.86 ± 0.04^{cd}	1.78 ± 0.03^{c}
	PM 30	2.39 ± 0.02^{bc}	2.53 ± 0.03^{a}	1.64 ± 0.01^{ef}	1.69 ± 0.02^{d}
$eO_3 \times eCO_2$	PDZM 31	2.40 ± 0.02^{bc}	2.11 ± 0.01^{ef}	2.18 ± 0.04^{b}	1.81 ± 0.002^{c}
	Pusa Bold	2.30 ± 0.03^{cd}	2.22 ± 0.01^{cde}	1.82 ± 0.02^{d}	1.67 ± 0.02^{de}
	PM 30	2.14 ± 0.01^{d}	2.24 ± 0.04^{cd}	1.56 ± 0.04^{f}	1.61 ± 0.04^{e}
Ambient	PDZM 31	2.65 ± 0.03^{a}	2.37 ± 0.01^{b}	2.39 ± 0.03^{a}	2.10 ± 0.01^{a}
	Pusa Bold	2.65 ± 0.02^{a}	2.33 ± 0.02^{bc}	2.39 ± 0.04^{a}	2.08 ± 0.02^{a}
	PM 30	2.49 ± 0.20^{ab}	2.62 ± 0.12^{a}	1.92 ± 0.01^{c}	1.80 ± 0.03^{c}
SEM		0.034	0.272	0.032	0.022
CD ($P<0.05$)		0.172	0.128	0.087	0.069
Treatment		***	***	***	***
Genotype		***	***	***	***
Treatment × Genotype		***	***	***	***

genotypes ($P \leq 0.001$), and treatment-genotype interactions ($P \leq 0.001$) across both seasons (Table 1). In the first season (2020–21), the highest seed length was recorded under ambient conditions (2.65 mm in PDZM 31) and elevated CO_2 (2.62 mm), whereas the lowest seed length was observed under elevated ozone (eO_3) in PM 30 (1.85 mm), followed by the interaction treatment in PM 30 (2.14 mm). Similarly, in the second season, the highest seed length was observed under ambient conditions (2.62 mm) and eCO_2 in PM 30 (2.53 mm), followed by the interaction treatment in PM 30 (2.37 mm). The lowest seed length was recorded under elevated ozone in PM 30 (2.03 mm) and PDZM 31 (2.07 mm).

In terms of seed width during the first season, the highest values were recorded under ambient conditions (2.39 mm in Pusa Bold), $eO_3 \times eCO_2$ (2.39 mm in PDZM 31), and eCO_2 (2.37 mm in PDZM 31). This was followed by ambient conditions (2.18 mm) and eO_3 in PDZM 31 (2.16 mm). The lowest seed width was observed under elevated ozone (1.40 mm in PM 30) and the interaction treatment (1.56 mm in PM 30), followed by elevated CO_2 (1.64 mm in PM 30) and elevated ozone (1.71 mm in Pusa Bold). Similar trends were observed in the second season (2021–22), where seed width decreased under elevated O_3 (1.15 mm in PM 30), followed by 1.61 mm in eO_3 (Pusa Bold) and interaction treatment in PM 30. Conversely, the highest seed width was recorded under ambient conditions (2.10 mm in PDZM 31 and 2.08 mm in Pusa Bold), followed by eCO_2 (1.99 mm in PDZM 31), interaction treatment (1.81 mm in PDZM 31 and 1.80 mm in PM 30), and eO_3 (1.78 mm in PDZM 31) and eCO_2 (Pusa Bold) (Table 1). Generally, crops exposed to eCO_2 experience changes in seed quality, including reductions in seed germination and vigour (Hampton *et al.* 2016, Lamichaney *et al.* 2019, Lamichaney *et al.* 2021, Lamichaney and Maity 2021). However, Lamichaney *et al.* (2022) reported contrary findings in mung bean, where seed length and width remained unaffected under eCO_2, except for seed thickness, which varied between 3–6% compared to ambient conditions.

Changes in seedling shoot and root length under different treatments: The seedling shoot length exhibited significant differences among treatments ($P \leq 0.001$), genotypes ($P \leq 0.001$), and treatment-genotype interactions ($P \leq 0.01$) as shown in Table 2. However, the interaction between treatment and genotype for seedling root length was found to be non-significant in Indian mustard. A decline in seedling shoot length was observed under elevated ozone, with values of 1.7 cm in Pusa Bold, 1.9 cm in PDZM 31, and 1.98 cm in PM 30, which were statistically on par. In contrast, the highest shoot length was recorded under elevated CO_2 in Pusa Bold (3.3 cm), followed by ambient conditions in PM 30 (2.95 cm), eCO_2 in PM 30 (2.73 cm), interaction treatment in PM 30 (2.65 cm), and ambient conditions in Pusa Bold (2.6 cm). Similarly, in the second season, shoot length was highest in eCO_2 (6.23 cm), followed

Table 2 Effect of eO_3, eCO_2, $eO_3 \times eCO_2$ and ambient on seedling shoot length (cm) and seedling root length (cm) of different genotypes

		Seedling shoot length (cm)		Seedling root length (cm)	
Treatment	Genotypes	2020–21	2021–22	2020–21	2021–22
eO_3	PDZM 31	1.90 ± 0.07^{de}	1.95 ± 0.03^{g}	3.80 ± 0.04^{e}	3.99 ± 0.04^{g}
	Pusa Bold	1.70 ± 0.45^{e}	2.00 ± 0.11^{fg}	4.15 ± 0.33^{de}	4.40 ± 0.22^{efg}
	PM 30	1.98 ± 0.11^{de}	4.93 ± 0.08^{b}	4.70 ± 0.12^{cd}	4.75 ± 0.23^{def}
eCO_2	PDZM 31	2.33 ± 0.16^{de}	2.45 ± 0.15^{def}	4.60 ± 0.04^{de}	4.70 ± 0.04^{def}
	Pusa Bold	3.30 ± 0.37^{a}	3.60 ± 0.22^{c}	6.70 ± 0.66^{a}	6.95 ± 0.48^{a}
	PM 30	2.73 ± 0.06^{bc}	6.23 ± 0.27^{a}	6.15 ± 0.31^{ab}	5.90 ± 0.23^{b}
$eO_3 \times eCO_2$	PDZM 31	1.95 ± 0.05^{de}	2.00 ± 0.06^{fg}	4.10 ± 0.04^{de}	4.20 ± 0.04^{fg}
	Pusa Bold	2.33 ± 0.10^{cd}	2.53 ± 0.27^{de}	4.58 ± 0.23^{de}	4.83 ± 0.23^{de}
	PM 30	2.65 ± 0.12^{bc}	5.08 ± 0.27^{b}	4.75 ± 0.18^{cd}	4.95 ± 0.21^{de}
Ambient	PDZM 31	2.00 ± 0.07^{de}	2.18 ± 0.05^{efg}	4.48 ± 0.06^{de}	4.54 ± 0.03^{efg}
	Pusa Bold	2.60 ± 0.07^{bc}	2.78 ± 0.09^{d}	5.43 ± 0.37^{bc}	5.68 ± 0.25^{bc}
	PM 30	2.95 ± 0.13^{ab}	6.08 ± 0.19^{a}	5.50 ± 0.26^{bc}	5.25 ± 0.12^{cd}
SEM		0.147	0.147	0.220	0.175
CD ($P<0.05$)		0.432	0.492	0.807	0.615
Treatment		***	***	***	***
Genotype		***	***	***	***
Treatment × Genotype		**	**	NS	NS

by ambient conditions (6.08 cm) > interaction treatment (eO_3 × eCO_2) (5.08 cm) > eO_3 (4.93 cm) in PM 30. For Pusa Bold, the seedling shoot length was highest under ambient conditions (2.78 cm) > eCO_2 (3.6 cm) > interaction (2.53 cm) > eO_3 (2.0 cm). In PDZM 31, the highest shoot length was recorded under eCO_2 (2.45 cm) > ambient (2.18 cm) > interaction (2.0 cm) > eO_3 (1.95 cm).

Seedling root length in both seasons followed a similar trend, with values highest under eCO_2 > ambient > interaction treatment (eO_3 × eCO_2) > eO_3 (Table 2). The rising atmospheric CO_2 concentration (Ambient + 200 ppm) has been reported to decrease seed vigour, negatively impacting germination in rice cultivars (*Oryza sativa* L.) (Chen *et al.* 2015). Our findings suggest that higher levels of O_3 and CO_2 significantly impact seed germination by inducing dormancy and increasing the occurrence of abnormal seedlings. Similarly, a study on mung bean (*Vigna radiata* L.) exposed to elevated CO_2 (600 ppm) showed that seed germination was reduced by 68–72%, while the proportion of hard seeds increased by 13–19% (Lamichaney *et al.* 2022). Furthermore, *Pinus sylvestris* seedlings exposed to elevated ozone (38.8 ± 10 ppb) exhibited a significant decline in shoot length, as reported by Kivimaenpaa *et al.* (2017).

From this study, it is concluded that seed germination traits (total seed germination percentage, speed of germination, uniformity in germination, seedling shoot and root length, seed length, and seed width) were significantly impacted in Indian mustard (PDZM 31, Pusa Bold, and PM 30) under varying climatic conditions of elevated ozone and carbon dioxide. Seed germination declined by 2–1% under elevated ozone, whereas it remained unchanged under elevated CO_2. Seed length decreased by 24% in PM 30, 12% in Pusa Bold, and 11.19% in PDZM 31. However, the adverse effects of elevated ozone were mitigated by elevated CO_2, as observed in the interaction treatment (eO_3 × eCO_2), where the reduction was 14% in PM 30, 10% in PDZM 31, and 9% in Pusa Bold. Similarly, seed width exhibited a significant decline of 20% under elevated ozone, but this reduction was partially compensated by 10% under interaction treatments. Thus, our findings confirm that future climate conditions involving increased tropospheric ozone and CO_2 enrichment will result in significant alterations in seed-related traits, with ozone having the most detrimental effects. Furthermore, documentation of physiological responses of seed-related traits under future climate conditions remains limited and requires further research. Also, future studies on metabolomics study in the seeds under changing climate conditions to know the response of primary and secondary metabolites and to bring out ozone-tolerant varieties through breeding and genomic research.

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