



Design and validation of a low-cost open-top chamber for plant climate change experiments

Ji Yeong Hwang^{1†}, Ha-Ryeong Lee^{1†}, Hyun Jun Park², Bo Eun Nam³, Jae Geun Kim^{2*} and Youngsung Joo^{1,4*}

¹School of Biological Sciences, Seoul National University, Seoul 08826, Republic of Korea

²Department of Biology Education, Seoul National University, Seoul 08826, Republic of Korea

³Research Institute of Basic Sciences, Seoul National University, Seoul 08826, Republic of Korea

⁴Institute of Data Innovation in Sciences, Seoul National University, Seoul 08826, Republic of Korea

ARTICLE INFO

Received October 30, 2025

Revised December 26, 2025

Accepted January 31, 2026

Published on February 25, 2026

*Corresponding author

Jae Geun Kim

E-mail jaegkim@snu.ac.kr

Youngsung Joo

E-mail yousjoo@snu.ac.kr

[†]These authors contributed equally to this work.

Abstract

Rising atmospheric CO₂ is a primary driver of ongoing climate change; however, plant responses to elevated CO₂ remain highly variable across species and functional traits. Given that CO₂ enrichment fundamentally modulates photosynthesis, water-use efficiency, and growth, controlled experiments are essential to quantify these responses under climate-relevant conditions. In this context, open-top chambers (OTCs) provide a practical and standardized approach to simulate elevated CO₂ environments in field settings. We describe a reproducible, low-cost OTC system and provide detailed protocols for its design, construction, calibration, and operation to facilitate widespread adoption. Performance validation confirmed that the system significantly elevated CO₂ concentrations compared to ambient levels (targeting the RCP4.5 concentration of ~540 ppm), while maintaining consistent temperature and humidity profiles across chambers. As a case study, we compared the physiological responses of the endemic plant *Leontopodium leiolepis* and the widespread native plant *Dendranthema zawadskii* var. *tenuisectum* under ambient and elevated CO₂ conditions. Elevated CO₂ significantly increased leaf gas-exchange rates in both species, demonstrating that the developed OTC system is effective in inducing distinct physiological shifts in plants. However, morphological growth traits remained unchanged, with neither species showing significant plasticity between ambient and elevated CO₂ conditions. Our OTC platform maintains environmental conditions while enabling precise regulation of CO₂ concentrations. By simulating realistic future CO₂ scenarios, the system effectively induces measurable physiological responses in plants, offering an accessible and reproducible framework for generating standardized trait datasets and empirically grounded sensitivity metrics.

Keywords: climate change simulation, *Dendranthema zawadskii* var. *tenuisectum*, elevated CO₂, *Leontopodium leiolepis*, methodological validation, open-top chamber, photosynthetic response

Introduction

Atmospheric carbon dioxide (CO₂) concentrations are rising at an unprecedented rate, primarily driven by anthropogenic activities. This accumulation of greenhouse gases has altered the global climate system, warming the atmosphere and oceans and increasing the frequency and intensity of extreme weather events. These complex climate changes strongly affect natural systems (IPCC 2023). Elevated atmospheric CO₂ profoundly affects plant morphology and physiology. It directly influences photosynthesis and respiration, which involve carbon fixation and carbon

efflux (Campbell et al. 1988; Gonzalez-Meler et al. 1996). These direct effects can alter the carbon and water balance of plants, causing secondary effects on growth and resource allocation (Sage 2002). Beyond plant biomass and yield (Cure and Acock 1986; Högy et al. 2009), elevated CO₂ also impacts developmental processes such as flowering (Ushio et al. 2014) and fruiting (Ito et al. 1999). Changes in morphological or chemical phenotypes can affect other components of the plant community (Rocheftort and Woodward 1992) and ultimately ecosystem processes (Baldrian 2017; Stam et al. 2014). The carbon assimilation rate, a direct response to atmospheric CO₂, may increase



(Ford and Thorne 1967) or decrease (Delucia et al. 1985) depending on the species. Thus, species-specific responses to elevated CO₂ vary widely (Lindroth et al. 1993).

Endemic species are taxa restricted to a defined geographic region. They typically have narrow geographic ranges and often exhibit narrow ecological tolerances or strong habitat specificity (Anderson 1994), making them poor dispersers and tightly linked to local environmental conditions (Burlakova et al. 2011). Due to these traits, endemic plants are expected to be particularly sensitive to climate change. In the Republic of Korea, while habitat characteristics and distribution patterns of the endemic flora are well documented (Chung et al. 2017, 2020; Kim et al. 2024), experimental quantification of plant responses to environmental factors such as temperature and moisture remains limited. Consequently, the vulnerability of Korean endemic species is often underestimated despite their restricted ecological niches (Cho et al. 2024).

We propose a reproducible mesocosm approach that simulates environmental conditions at low cost. While climate change-associated mesocosms are typically operated as large-scale infrastructures with significant constraints on scale and cost (Roy et al. 2021; Schmidt et al. 2021), an open-top chamber (OTC) offers a low-cost, small-footprint, and laboratory-compatible mesocosm solution. OTCs use transparent sidewalls and an open top to allow near-natural air exchange, while blowers maintain uniform CO₂ distribution within the chamber. This configuration supports the efficient investigation of physiological responses under near-natural conditions (Macháčová 2010). OTCs have been widely applied to test plant responses to climate change, including aboveground biomass, shoot density, and shoot height (Drake et al. 1989; Leadley and Drake 1993; Messerli et al. 2015).

Here, we describe the design, construction, calibration, and operation of a low-cost OTC system and demonstrate how it generates standardized trait and physiological data. As a case study, we quantified growth traits and photosynthetic performance of *Leontopodium leirolepis* (a Korean endemic plant narrowly distributed in highland areas) and *Dendranthema zawadskii* var. *tenuisectum* (a Korean native plant widely distributed at high altitudes). This multifactorial OTC pipeline enables controlled, climate-relevant experiments to compare species responses under standardized conditions.

Materials and Methods

Chamber construction and CO₂ concentration regulation

Schematic diagrams and photographs of the OTC experimental setup are shown in Figure 1. The framework of the experimental chamber was a regular hexagonal prism,

adapted from the design by Messerli et al. (2015). The overall dimensions of the structure were 1,200 mm * 1,039 mm * 1,020 mm (Width * Depth * Height), with each of the six side panels measuring 600 mm in width. The frame was fabricated from SUS304 stainless steel (containing 18% chromium and 8% nickel), and transparent polycarbonate plates were used for the side walls. To facilitate access, one panel was hinged with a latch to serve as an access door.

The CO₂ was supplemented by mixing ambient air with high-purity CO₂. The CO₂ gas was supplied from individual gas tanks (99.999% purity, 40 L, DAESUNG, Seoul, Korea). This method elevates the atmospheric CO₂ concentration within the chamber while avoiding direct exposure of concentrated CO₂. Control chambers received only ambient air (without CO₂ enrichment) through the same delivery hardware to account for any potential effects of the air injection system itself.

Air was supplied through a hollow hexagonal manifold assembled from 100 mm-diameter PVC (600 mm length; cross-sectional area = 7,854 mm²). The manifold face directed toward the chamber interior was perforated with air holes (hole area = 19.63 mm²) at 30 mm intervals to ensure uniform distribution. The target inlet velocity was ≥ 566 mm s⁻¹, powered by a single-phase AC blower (220 V, 60 Hz) sized to meet the required flow rate.

The CO₂ concentration was maintained using a custom-built CO₂ supply control system (SH-MVG260-003; SOHA TECH, Seoul, Korea) that operated on an on/off control loop. The flow of CO₂ from the gas tank was controlled by a regulator (G250-150-K22R; VICTOR, Chesterfield, MO, USA). An integrated sensor (SH-VT260-003; SOHA TECH) continuously monitored the internal CO₂, air temperature, and humidity. CO₂ injection was triggered when the CO₂ concentration fell below a lower threshold and stopped upon reaching the upper threshold. The lower and upper threshold can be set to define a 20% range around the target concentration. However, these thresholds should be optimized based on environmental conditions, such as internal temperature and air circulation at the open top of the chamber.

Installation, environmental control, and data logging

Since the current OTCs are not waterproof, all chambers were operated inside a glasshouse protected from precipitation. The glasshouse was ventilated by open windows, internal circulation fans, and an external exhaust system. This environment resulted in an internal temperature approximately 2°C higher than the external ambient temperature. Within a chamber, CO₂, air temperature, and relative humidity were measured every minute (RN400-T2PM-RG23; Dekist, Yongin, Korea). Values were written to SD cards at 10-minute intervals and subsequently organized into a tabular format for analysis.

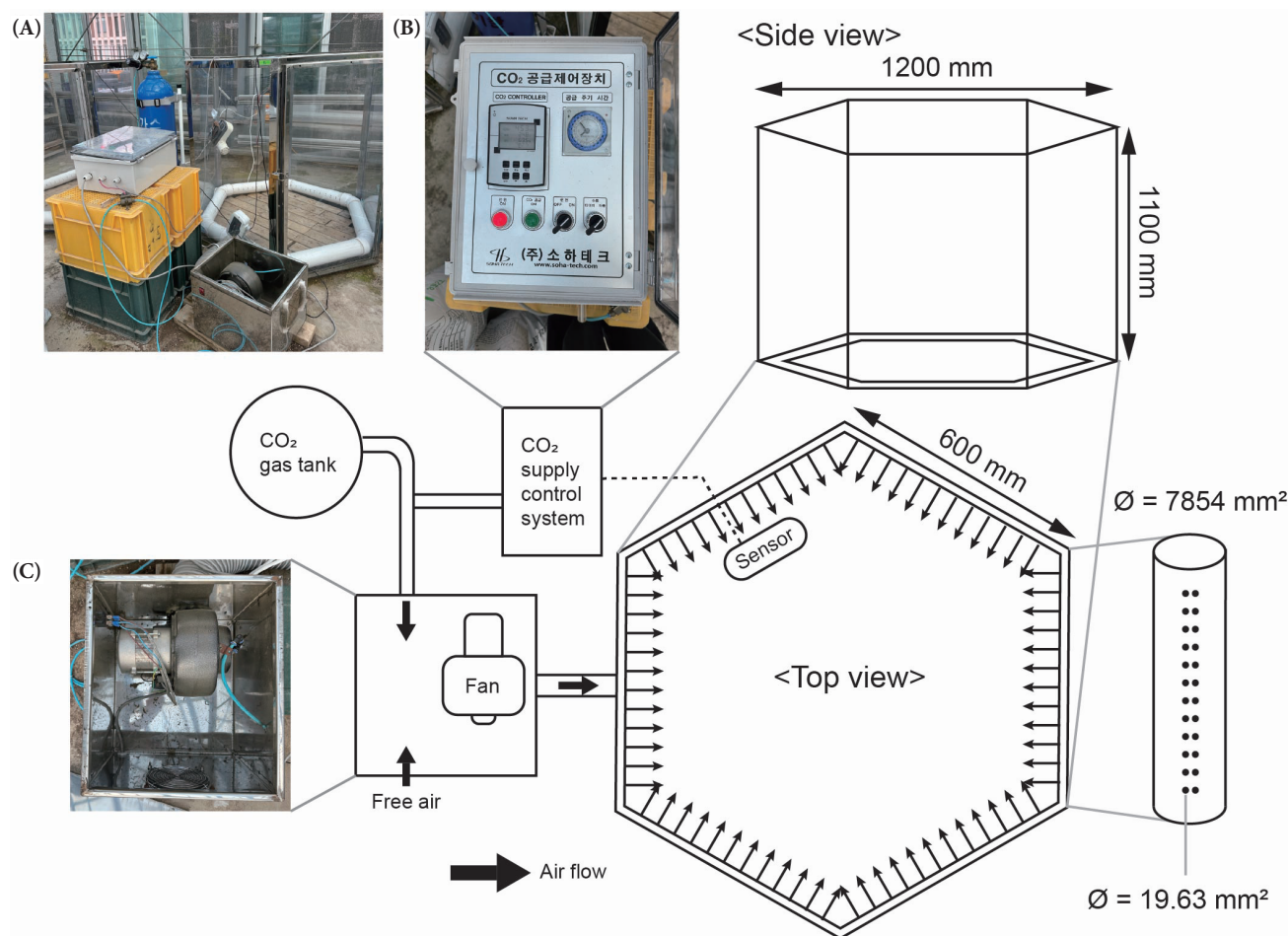


Fig. 1 Schematic diagrams and photographs of the open-top chamber (OTC) experimental setup. (A) Overall view of the system, including the OTC frame, carbon dioxide (CO₂) gas tank, and CO₂ supply control unit, (B) photograph of the CO₂ supply control system, and (C) photograph of the CO₂ ventilation fan system.

Routine maintenance is straightforward: monthly CO₂ leak checks and two-point sensor calibration, quarterly blower filter cleaning and hose inspection, and annual replacement of flexible tubing and regulator seals. The controller fails safe (CO₂ valve closed) upon power loss or sensor error, and chambers can be returned to ambient conditions within minutes.

Validation of OTC performance

To comprehensively validate the performance of the OTC system, we assessed both the stability of environmental control and the biological applicability of the system.

First, to assess the homogeneity of environmental conditions and the precision of CO₂ regulation, we intensively monitored CO₂ concentration, air temperature, and relative humidity across all four chambers from June 17 to June 26, 2025. During this period, the chambers were fully occupied with potted plants to simulate the microclimate of a typical experimental deployment. Ambient CO₂ chambers were maintained without manipulation, whereas elevated CO₂ chambers were actively regulated to maintain a target concentration of 540 ppm (corresponding to the RCP4.5

scenario). Data were analyzed to confirm that the system could maintain distinct CO₂ regimes while minimizing chamber-specific variations in temperature and humidity.

To further verify the system's application, in a plant-containing mesocosm, a biological validation experiment was conducted on the rooftop of the College of Education, Building 9, Seoul National University. We selected two *Asteraceae* species with contrasting distributions: *L. leiolepis*, a Korean endemic species restricted to high-altitude rock crevices (Lee et al. 2016), and *D. zawadskii* var. *tenuisectum*, a widespread native species found on sunny mountain slopes (Flora of Korea Editorial Committee 2020). These species were chosen to test the feasibility of the OTC system for comparative physiological studies independent of their natural geographic distributions.

Nursery-grown plants were transplanted from the glass-house into 11 cm pots (11 cm in diameter, 11 cm in height) filled with a volumetric ratio of 2:1 mixture of sand (Ecosand, Busan, Korea) and topsoil (Nongwoo BIO, Suwon, Korea). Plants were grown in the OTCs for 53 days under two CO₂ regimes (ambient: ~420 ppm; elevated: ~540 ppm), representing RCP4.5 end-of-century projection (IPCC 2014). We

used two replicate chambers per CO₂ treatment, with 15 plants per chamber. Plant growth responses were determined by measuring plant growth traits (leaf number and longest leaf length) at intervals of approximately two weeks. Net CO₂ assimilation rates were measured using a portable gas-exchange system (GFS-3000; Heinz Walz GmbH, Effeltrich, Germany).

Statistical analysis

To assess the homogeneity of OTC system performance, we selected statistical models based on the response distribution and model diagnostics. To further verify consistency in environmental variability between replicate chambers within each CO₂ treatment, the homogeneity of variances was assessed using Levene's test (function `leveneTest` in the `car` package). For environmental factors-CO₂ concentration, air temperature, and relative humidity-Generalized Linear Models (GLMs; function `glm`) were used to evaluate the effects of CO₂ treatment and chamber identity.

Plant biological parameters were analyzed using models tailored to their specific data structures. Plant assimilation rate was analyzed using a Linear Model (LM; function `lm`), as residual diagnostics indicated approximately normal and homoscedastic errors without the need for random effects. In contrast, leaf number and longest leaf length were analyzed using Generalized Linear Mixed-Effects Models (GLMMs; function `glmer`), with measurement date included as a random intercept to account for temporal variation. Leaf number was modeled with a Poisson distribution, whereas longest leaf length was modeled with a Gamma distribution (log link).

Post-hoc pairwise comparisons of estimated marginal means were conducted with the `emmeans` package, applying a Sidak adjustment to control the family-wise error rate, and compact letter displays were used to summarize group differences (Hothorn et al. 2025; Lenth 2025). All analyses were performed in R v. 4.4.3 (R Core Team 2025).

Results

OTC build cost and system performance

Excluding the cost of consumable CO₂, the total construction cost for the four OTC units was approximately 10.5 million KRW (~7,400 USD). This cost covers two chambers equipped with an external gas supply for elevated CO₂ conditions and two control chambers supplied with ambient air. A detailed breakdown of the expenses is provided in Table S1. On average, one 40 L tank of 99.999% CO₂ gas was consumed per chamber every ten days, though the consumption rate varied depending on the ambient temperature within the glasshouse.

During the OTC performance validation, mean CO₂ concentrations (mean $\pm$ SE) were 446.2 $\pm$ 4.0 ppm in Ambient Chamber 1, 455.8 $\pm$ 2.5 ppm in Ambient Chamber 2, 554 $\pm$ 17 ppm in Elevated Chamber 1, and 519.2 $\pm$ 7.6 ppm in Elevated Chamber 2 (Fig. 2A). Mean CO₂ differed significantly between the ambient and elevated CO₂ treatments ($p < 0.001$), whereas no significant differences were detected between chambers within the same CO₂ treatment. In contrast, mean air temperature and relative humidity remained comparable between CO₂ treatments throughout the experimental period. Mean temperature was 25.27 $\pm$ 0.70°C in Ambient Chamber 1, 26.70 $\pm$ 0.71°C in Ambient Chamber 2, 25.65 $\pm$ 0.70°C in Elevated Chamber 1, and 25.90 $\pm$ 0.71°C in Elevated Chamber 2 (Fig. 2B). Mean relative humidity was 73.8 $\pm$ 4.3% in Ambient Chamber 1, 68.1 $\pm$ 4.0% in Ambient Chamber 2, 73.3 $\pm$ 4.2% in Elevated Chamber 1, and 71.5 $\pm$ 3.9% in Elevated Chamber 2 (Fig. 2C), with no significant differences between CO₂ treatments. To assess homogeneity of variances between ambient and elevated chamber, we conducted Levene's test and found no statistically significant differences in variance for either temperature or humidity. Natural diurnal variations in temperature and humidity were observed within the OTCs, reflecting the daily temperature fluctuations in Korea. Despite these fluctuations, the CO₂ concentration in the elevated CO₂ chambers was consistently

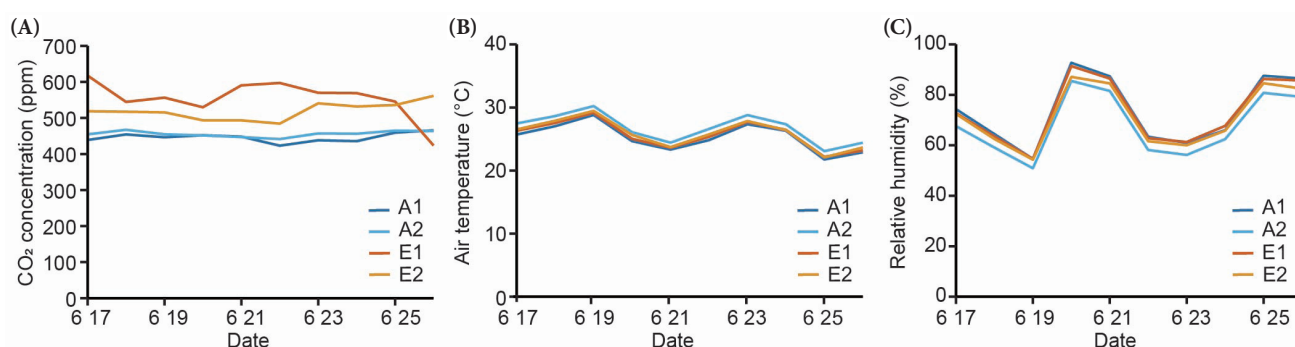


Fig. 2 Environmental conditions in the open-top chambers (OTCs) during the validation experiment (June 17–26, 2025). (A) Carbon dioxide (CO₂) concentration (ppm), (B) internal chamber air temperature (°C), and (C) internal chamber relative humidity (%) measured in each chamber. Ambient and elevated CO₂ treatments each had two replicate chambers. A1: Ambient Chamber 1; A2: Ambient Chamber 2; E1: Elevated Chamber 1; E2: Elevated Chamber 2.

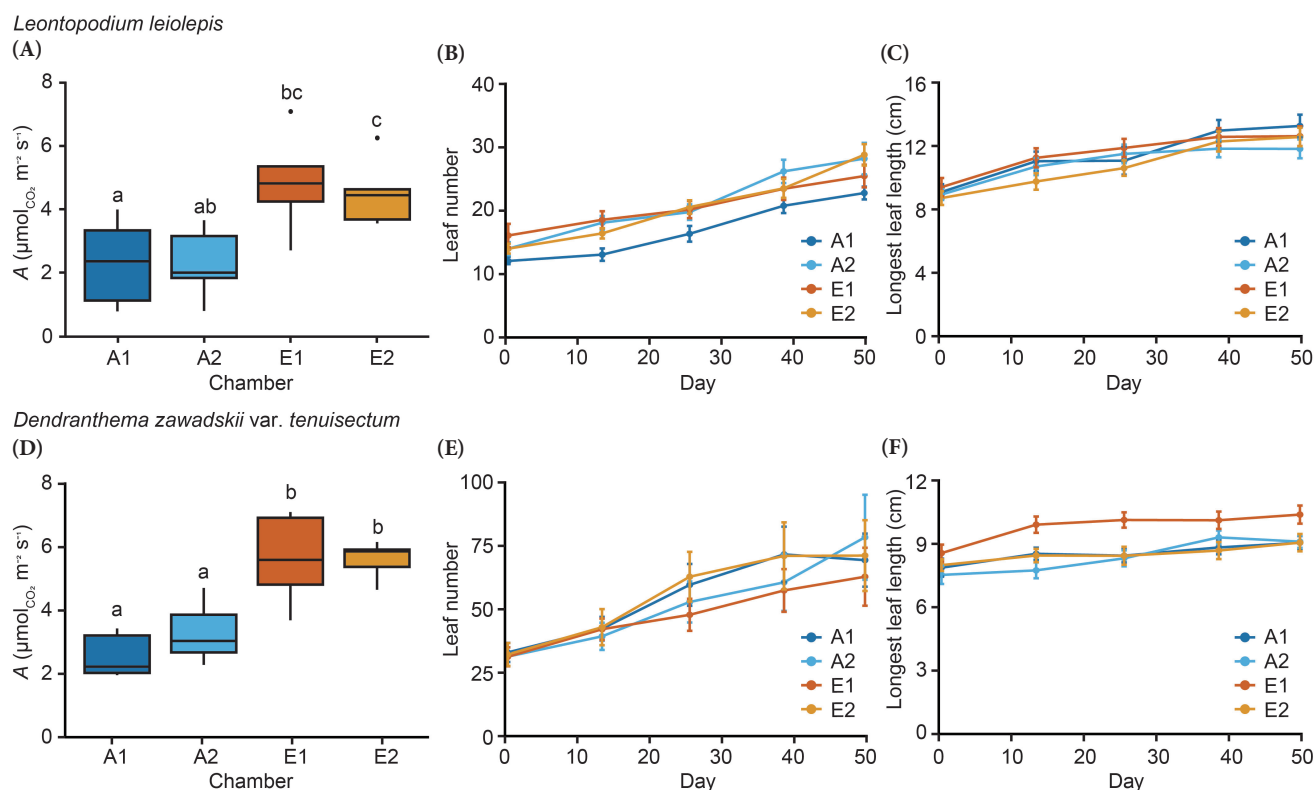


Fig. 3 Photosynthesis and growth responses of the endemic *Leontopodium leiolepis* (A–C) and the native *Dendranthema zawadskii* var. *tenuisectum* (D–F). Measurements shown are: (A, D) net assimilation rate (A, $\mu\text{mol m}^{-2} \text{ s}^{-1}$); (B, E) leaf number; (C, F) longest leaf length (cm). Different letters indicate statistically significant differences between groups ($p < 0.05$). A1: Ambient Chamber 1; A2: Ambient Chamber 2; E1: Elevated Chamber 1; E2: Elevated Chamber 2.

maintained at an elevated level compared to the ambient CO_2 chambers. Table S2 presents a representative diurnal profile consisting of hourly averaged logger data.

OTC-based climate change simulation experiment

Net CO_2 assimilation rates increased significantly under elevated CO_2 in both *L. leiolepis* and *D. zawadskii* var. *tenuisectum* ($p < 0.001$). *Dendranthema zawadskii* var. *tenuisectum* showed no significant differences among chambers (Fig. 3D), whereas *L. leiolepis* exhibited minor, non-significant chamber-to-chamber variation (Fig. 3A). Regarding growth traits, *D. zawadskii* var. *tenuisectum* showed no significant effects of CO_2 treatment or chamber on the growth of leaf number or longest leaf length. For *L. leiolepis* leaf number, however, a significant chamber effect was detected ($p = 0.035$).

Discussion

Demonstrated OTC system performance

The logger data confirmed the effective operation of the OTCs, showing a significantly higher CO_2 concentration but no significant differences in temperature or humidity between chamber settings (Fig. 2). Furthermore, the increased net assimilation rate in both plant species, *L. leio-*

lepis and *D. zawadskii* var. *tenuisectum*, under CO_2 enrichment demonstrates that the treatment was sufficient to elicit a physiological response (Fig. 3A, D). However, no significant responses were detected in most growth parameters of either species. Overall, the combined physiological and growth responses indicate that the OTC system successfully established distinct CO_2 environments capable of inducing expected physiological shifts, even when short-term growth metrics did not diverge strongly. This pattern is consistent with the idea that growth integrates multiple constraints and may lag behind immediate physiological changes (Kirschbaum 2011; Leakey et al. 2009).

Accordingly, the CO_2 -driven increase in assimilation-together with generally limited chamber-to-chamber variation-provides a baseline for subsequent CO_2 experiments targeting longer exposure periods and broader functional responses. In *L. leiolepis*, net assimilation showed a small, non-significant chamber effect, whereas leaf number differed among chambers. These chamber-associated signals were not evident in the remaining traits or in *D. zawadskii* var. *tenuisectum*, but they highlight the need to account for potential chamber effects in future experiments, particularly for *L. leiolepis*, by extending exposure duration and/or increasing replication across chambers.

Applicability and limitation of the OTC system

Our OTC design differs from previous models, such as those described by Messerli et al. (2015), particularly in the choice of materials. We constructed the frames using stainless steel, which offers superior durability and resistance to contamination. Additionally, our design features a bottom-up airflow system, which facilitates efficient air circulation and ensures a uniform distribution of CO₂ throughout the chamber. However, a trade-off exists between robustness and portability; the increased weight of stainless steel restricts mobility in field settings. Therefore, researchers should carefully select materials that align with their specific experimental objectives. From a cost perspective, since steel framing constituted a major fraction of the build cost (Table S1), future iterations could be assembled more economically using aluminum extrusion, PVC, or treated timber frames without altering the fluid-handling architecture. We also acknowledge a limitation in the CO₂ regulation mechanism. Our system relies on solenoid valves for on/off control of CO₂ supply. However, this method can be challenging under high-temperature conditions that drive rapid air circulation, making precise modulation difficult and potentially leading to increased fluctuation in CO₂ concentrations. To mitigate this, manual calibration of the pure CO₂ inflow rate is required to ensure stability. These OTC trials provide one of the first experimental datasets quantifying trait and defense responses of a narrowly distributed Korean endemic under climate-relevant CO₂ conditions. Herbaceous individuals ($n = 15$ per species per chamber) were monitored throughout the experiment; from day 0 to day 53, mean height increased from 7.18 to 9.21 cm in *L. leiolepis*, and from 8.15 to 19.78 cm in *D. zawadskii* var. *tenuisectum*. Although OTCs are not practical for large trees or population-scale manipulations (Macháčová 2010), they are particularly effective for herbaceous plants and juvenile stages of woody or vine species across developmental stages (Kim et al. 2025; Park et al. 2021, 2022).

Conclusions

OTCs provide a valuable lab-scale methodology for creating mesocosms that simulate climate change, allowing for the direct observation of plant responses. In this study, we constructed and utilized four OTCs with stainless steel frames. During the validation period, mean CO₂ concentrations in the OTCs were maintained at target levels corresponding to the current (ambient) and RCP4.5 (elevated) scenarios, averaging 477.0 ± 2.7 ppm and 610 ± 14 ppm, respectively. This environment was sufficient to elicit measurable physiological responses in plants. The resulting trait data provide direct, empirical metrics of species-specific sensitivity to elevated CO₂ and associated functional responses under climate-relevant conditions.

Abbreviations

CO₂: Carbon dioxide

OTCs: Open-top chambers

Acknowledgements

We thank Yun Won Park (School of Biological Sciences, Seoul National University) for assistance with plant growth measurements.

Authors' contributions

JYH conducted the simulation experiments using OTCs and contributed to investigation, formal analysis, and writing (original draft). HRL managed the overall operation and maintenance of the chambers and contributed to investigation, visualization, and writing (original draft). HJP and BEN developed the initial concept and design. JGK and YJ provided overall supervision and writing (review & editing). All authors read and approved the final manuscript.

Funding

This research was supported by the project "Establishment of Biodiversity Assessment System for Carbon Sink Ecosystems (NIE-C-2024-111)" conducted by the National Institute of Ecology with funding from the Ministry of Environment, Republic of Korea.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Supplementary Information

Supplementary information accompanies this paper at <https://doi.org/10.5141/jee.25.096>.

Table S1. Cost breakdown for the construction of four open-top chambers. **Table S2.** Representative hourly averaged temperature, relative humidity (%), and CO₂ concentration (ppm) for a single day, calculated from raw data recorded on June 25, 2025.

References

- Anderson S. Area and endemism. *Q Rev Biol.* 1994;69(4):451-71.
- Baldrian P. Forest microbiome: diversity, complexity and dynamics. *FEMS Microbiol Rev.* 2017;41(2):109-30. <https://doi.org/10.1093/femsre/fuw040>.

- Burlakova LE, Karatayev AY, Karatayev VA, May ME, Bennett DL, Cook MJ. Endemic species: contribution to community uniqueness, effect of habitat alteration, and conservation priorities. *Biol Conserv*. 2011;144(1):155-65. <https://doi.org/10.1016/j.biocon.2010.08.010>.
- Campbell WJ, Allen LH Jr, Bowes G. Effects of CO₂ concentration on rubisco activity, amount, and photosynthesis in soybean leaves. *Plant Physiol*. 1988;88(4):1310-6. <https://doi.org/10.1104/pp.88.4.1310>.
- Cho YC, Seol J, Lim CH. Climate-induced distribution dynamics and niche adaptation of South Korean endemic plants across the Korean Peninsula. *Sci Rep*. 2024;14(1):22253. <https://doi.org/10.1038/s41598-024-73569-4>.
- Chung GY, Chang KS, Chung J, Choi HJ, Paik W, Hyun J. A checklist of endemic plants on the Korean Peninsula. *Korean J Pl Taxon*. 2017;47(3):264-88. <https://doi.org/10.11110/kjpt.2017.47.3.264>.
- Chung J, Shin J, Kim H. Diversity of vascular plants native to the Ulleungdo and Dokdo Islands in Korea. *J Asia Pac Biodivers*. 2020;13(4):701-8. <https://doi.org/10.1016/j.japb.2020.08.001>.
- Cure JD, Acock B. Crop responses to carbon dioxide doubling: a literature survey. *Agric For Meteorol*. 1986;38(1-3):127-45. [https://doi.org/10.1016/0168-1923\(86\)90054-7](https://doi.org/10.1016/0168-1923(86)90054-7).
- Delucia EH, Sasek TW, Strain BR. Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. *Photosynth Res*. 1985;7(2):175-84. <https://doi.org/10.1007/BF00037008>.
- Drake BG, Leadley PW, Arp WJ, Nassiry D, Curtis PS. An open top chamber for field studies of elevated atmospheric CO₂ concentration on saltmarsh vegetation. *Funct Ecol*. 1989;3(3):363-71. <https://doi.org/10.2307/2389377>.
- Flora of Korea Editorial Committee. Flora of Korea. Volume 6c-2: Asteridae: Asteraceae (2). Incheon: National Institute of Biological Resources, Ministry of Environment; 2020.
- Ford MA, Thorne GN. Effect of CO₂ concentration on growth of sugar-beet, barley, kale, and maize. *Ann Bot*. 1967;31(4):629-44. <https://doi.org/10.1093/oxfordjournals.aob.a084168>.
- Gonzalez-Meler MA, Ribas-Carbo M, Siedow JN, Drake BG. Direct inhibition of plant mitochondrial respiration by elevated CO₂. *Plant Physiol*. 1996;112(3):1349-55. <https://doi.org/10.1104/pp.112.3.1349>.
- Hothorn T, Bretz F, Westfall P. multcomp: simultaneous inference in general parametric models. R package. 2025. <https://CRAN.R-project.org/package=multcomp>. Accessed 22 Oct 2025.
- Högy P, Wieser H, Köhler P, Schwadorf K, Breuer J, Franzaring J, et al. Effects of elevated CO₂ on grain yield and quality of wheat: results from a 3-year free-air CO₂ enrichment experiment. *Plant Biol (Stuttg)*. 2009;11 Suppl 1:60-9. <https://doi.org/10.1111/j.1438-8677.2009.00230.x>.
- IPCC. Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva: IPCC; 2014.
- IPCC. Climate change 2023: synthesis report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva: IPCC; 2023.
- Ito J, Hasegawa S, Fujita K, Ogasawara S, Fujiwara T. Effect of CO₂ enrichment on fruit growth and quality in Japanese pear (*Pyrus serotina* Reheder cv. Kosui). *Soil Sci Plan Nutr*. 1999;45(2):385-93. <https://doi.org/10.1080/00380768.1999.10409352>.
- Kim E, Lee S, Son S, Lee H. A study on the genetic variations and germination characteristics of *Rhododendron sohayakiense* to prepare for climate change threat. *Forests*. 2024;15(2):224. <https://doi.org/10.3390/f15020224>.
- Kim S, Park SH, Nam BE, Joo Y, Kim JG. Elevated CO₂ alters age-dependent variation in secondary metabolites, C/N ratio and growth of perennial herb, *Aristolochia contorta*. *Sci Total Environ*. 2025;991:179929. <https://doi.org/10.1016/j.scitotenv.2025.179929>.
- Kirschbaum MUF. Does enhanced photosynthesis enhance growth? Lessons learned from CO₂ enrichment studies. *Plant Physiol*. 2011;155(1):117-24. <https://doi.org/10.1104/pp.110.166819>.
- Leadley PW, Drake BG. Open top chambers for exposing plant canopies to elevated CO₂ concentration and for measuring net gas exchange. *Vegetatio*. 1993;104:3-15. <https://doi.org/10.1007/bf00048141>.
- Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR. Elevated CO₂ effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *J Exp Bot*. 2009;60(10):2859-76. <https://doi.org/10.1093/jxb/erp096>.
- Lee DH, Park JS, Choi BH. A taxonomic review of Korean *Leontopodium* R. Br. ex Cassini (Asteraceae). *Korean J Pl Taxon*. 2016;46(2):149-62. <https://doi.org/10.11110/kjpt.2016.46.2.149>.
- Lenth R. emmeans: estimated marginal means, aka least-squares means. R package. 2025. <https://CRAN.R-project.org/package=emmeans>. Accessed 22 Oct 2025.
- Lindroth RL, Kinney KK, Platz CL. Responses of deciduous trees to elevated atmospheric CO₂: productivity, phytochemistry, and insect performance. *Ecology*. 1993;74(3):763-77. <https://doi.org/10.2307/1940804>.
- Macháčová K. Open top chamber and free air CO₂ enrichment - approaches to investigate tree responses to elevated CO₂. *iForest*. 2010;3(4):102-5. <https://doi.org/10.3832/ifor0544-003>.
- Messerli J, Bertrand A, Bourassa J, Bélanger G, Castonguay Y, Tremblay G, et al. Performance of low-cost open-top chambers to study long-term effects of carbon dioxide and climate under field conditions. *Agron J*. 2015;107(3):916-20. <https://doi.org/10.2134/agronj14.0571>.
- Park HJ, Nam BE, Lee G, Kim SG, Joo Y, Kim JG. Ontogeny-dependent effects of elevated CO₂ and watering frequency on interaction between *Aristolochia contorta* and its herbivores. *Sci Total Environ*. 2022;838:156065. <https://doi.org/10.1016/j.scitotenv.2022.156065>.
- Park HJ, Nam BE, Moon SY, Kim SG, Joo Y, Kim JG. Reduced host plant growth and increased tyrosine-derived secondary metabolites under climate change and negative consequences on its specialist herbivore. *Sci Total Environ*. 2021;759:143507. <https://doi.org/10.1016/j.scitotenv.2020.143507>.
- R Core Team. R: a language and environment for statistical computing. R Foundation for Statistical Computing. 2025. <https://www.R-project.org/>. Accessed 22 Oct 2025.
- Roy J, Rineau F, De Boeck HJ, Nijs I, Pütz T, Abiven S, et al. Ecotrons: powerful and versatile ecosystem analysers for ecology, agronomy and environmental science. *Glob Chang Biol*. 2021;27(7):1387-407. <https://doi.org/10.1111/gcb.15471>.
- Rocheftort L, Woodward FI. Effects of climate change and a doubling of CO₂ on vegetation diversity. *J Exp Bot*. 1992;43(8):1169-80. <https://doi.org/10.1093/jxb/43.8.1169>.

- Sage RF. How terrestrial organisms sense, signal, and respond to carbon dioxide. *Integr Comp Biol*. 2002;42(3):469-80. <https://doi.org/10.1093/icb/42.3.469>.
- Schmidt A, Hines J, Türke M, Buscot F, Schädler M, Weigelt A, et al. The iDiv Ecotron-a flexible research platform for multitrophic biodiversity research. *Ecol Evol*. 2021;11(21):15174-90. <https://doi.org/10.1002/ece3.8198>.
- Stam JM, Kroes A, Li Y, Gols R, van Loon JJ, Poelman EH, et al. Plant interactions with multiple insect herbivores: from community to genes. *Annu Rev Plant Biol*. 2014;65:689-713. <https://doi.org/10.1146/annurev-arplant-050213-035937>.
- Ushio A, Hara H, Fukuta N. Promotive effect of CO₂ enrichment on plant growth and flowering of *Eustoma grandiflorum* (Raf.) Shinn. under a winter culture regime. *J Japan Soc Hort Sci*. 2014;83(1):59-63. <https://doi.org/10.2503/jjshs1.ch-040>.