

Cultivar-dependent differences in soybean N₂O emissions under wet, nitrogen-limited conditions: an eight-month pot experiment

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Research Article

Keywords: diurnal variation, greenhouse gas, post-harvest emission, soil moisture, transpiration

Posted Date: September 15th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-11030148/v1>

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Additional Declarations: The authors declare no competing interests.

Abstract

Nitrous oxide (N_2O) emissions from soybean cultivation are strongly influenced by soil and environmental conditions, yet the importance of cultivar differences remains poorly understood. We hypothesized that high-yield soybean cultivars with greater biomass production would exhibit higher N_2O emissions. To test this hypothesis, we quantified N_2O fluxes from pots cultivated with four commercially relevant soybean cultivars (two standard cultivars and two high-yield cultivars) over an eight-month period including harvest and a final drainage event under persistently wet, nitrogen-limited soil conditions. Diurnal variations and short-term responses to light-off were also examined to assess the role of plant physiological activity in N_2O emissions. N_2O emissions were low during the growth period but increased markedly after harvest. Interestingly, one of the high-yield cultivars generally exhibited relatively low N_2O emissions after harvest. Although cultivar differences were not detected during the growth period, shorter time-scale experiments suggested that plant physiological activity, particularly transpiration, played an important role in N_2O emissions. N_2O emissions decreased by more than half with the transition from light to dark conditions, coinciding with decreases in transpiration, despite minimal changes in soil temperature. Our findings suggest that cultivar differences in N_2O emissions may exist even among commercially relevant soybean cultivars and that high-yield cultivars do not necessarily exhibit higher N_2O emissions.

1. Introduction

Nitrous oxide (N_2O) is a potent greenhouse gas with a global warming potential approximately 273 times greater than that of CO_2 over a 100-year time horizon (IPCC, 2021). Agricultural soils are a major source of atmospheric N_2O because microbial nitrification and denitrification are stimulated by nitrogen inputs from fertilizers and plant residues under favorable soil moisture conditions (Butterbach-Bahl et al., 2013; Tian et al., 2024).

Soybean (*Glycine max* L.) is one of the world's most important legume crops and plays a major role in global protein and oil production (FAO, 2026). Although soybean typically receives little or no nitrogen fertilizer, biological nitrogen fixation supplies substantial amounts of nitrogen to the cropping system (Peoples et al., 2009; Salvagiotti et al., 2008). Consequently, soybean cultivation can contribute to N_2O emissions through nitrogen cycling during plant growth and decomposition of roots and crop residues after harvest (Della Chiesa et al., 2024; Inaba et al., 2012; Uchida and Akiyama, 2013). Reducing N_2O emissions from soybean cultivation is therefore important for developing climate-smart agricultural practices, and identifying cultivars with lower emission potential may contribute to this goal.

Most previous studies have focused on environmental and management controls of N_2O emissions, including soil moisture, fertilization, and residue management (Butterbach-Bahl et al., 2013). In contrast, potential cultivar differences in N_2O emissions have received limited attention. To our knowledge, few studies have directly examined cultivar-dependent variation in N_2O emissions from soybean (Kim et al.,

2005). This knowledge gap is important because recent breeding efforts have produced high-yield soybean cultivars with greater biomass production, potentially altering nitrogen cycling. Greater biomass may increase N₂O emissions through at least two pathways. First, greater root biomass may increase substrate availability for N₂O production by increasing carbon and nitrogen inputs to the soil. Second, greater aboveground biomass may enhance plant-mediated N₂O emissions through greater whole-plant transpiration (Chang et al., 1998; Zou et al., 2005). Consequently, high-yield cultivars could potentially exhibit greater N₂O emissions than standard cultivars. However, experimental evidence supporting this hypothesis remains scarce.

To test this hypothesis, we quantified N₂O emissions from four commercially relevant soybean cultivars, including two standard cultivars and two recently developed high-yield cultivars. To isolate cultivar effects from environmental variation, cultivars were evaluated in a controlled-environment chamber under standardized, persistently wet, nitrogen-limited conditions. N₂O fluxes were monitored throughout plant growth, post-harvest incubation, and a subsequent drainage period over more than eight months. In addition, short-term (diurnal and light-off) experiments were conducted to explore the contribution of plant physiological activity, particularly transpiration, to N₂O fluxes during the growing period, thereby providing mechanistic insight into how cultivar differences in N₂O emissions may emerge.

2. Materials and methods

2.1. Plant cultivation

A pot experiment was conducted in a controlled-environment chamber. Soil used for the pot experiment was collected from an experimental paddy field of NARO in Tsukubamirai, Ibaraki, Japan. The soil was classified as a clay loam according to the International Society of Soil Science textural classification (16.3% coarse sand, 32.3% fine sand, 28.5% silt, and 22.9% clay) with a pH(H₂O) of 5.7, total C of 20.3 g kg⁻¹, total N of 1.5 g kg⁻¹, available N of 57 mg kg⁻¹, available P₂O₅ of 101 mg kg⁻¹, and a cation exchange capacity of 13.4 cmol(+) kg⁻¹. Each pot (upper diameter, 21 cm; lower diameter, 18 cm; height, 27 cm) was filled with 7.4 kg of air-dried soil with 2.5 g pot⁻¹ of a PK fertilizer (20% citric-acid-soluble P₂O₅, 5% water-soluble P₂O₅, 4% citric-acid-soluble MgO, and 2% K₂O). The fertilizer was applied to the lower and middle portions of the soil profile (1.5 and 1.0 g pot⁻¹, respectively). Nitrogen fertilizer was not applied.

We sowed four soybean cultivars (Enrei, Sachiutaka, Sorahibiki, and Soramizuki) on 11 December 2024. Sorahibiki and Soramizuki were included as recently developed high-yielding cultivars in Japan (Kato et al., 2023; Shimamura et al., 2025). Four replicate pots were prepared for each cultivar and randomly arranged in a controlled-environment chamber. After the first true leaf had fully expanded, pots were maintained under persistently wet conditions by submerging their bases in 0.3–1.6 cm of water. Soybeans were grown under a 14-h photoperiod with day/night temperatures of approximately 25/21°C. Flowering occurred between 11 and 14 January 2025 in all cultivars except Soramizuki, which flowered

approximately one week later. Following flowering, the photoperiod was reduced to 12 h and the daytime temperature was increased to 28°C to promote reproductive development and maturation. Plants were harvested on 14 April 2025. Drainage was initiated on 23 July 2025. For subsequent analyses, the experimental period was divided into three phases: Phase 1, from sowing to harvest (plant growth period under wet conditions); Phase 2, from harvest to drainage (post-harvest period under wet conditions); and Phase 3, after drainage initiation (post-drainage period).

2.2. Soil environmental measurements

Soil temperature and volumetric water content were monitored using TEROS-12 sensors (METER Group, Pullman, WA, USA). One representative pot per cultivar was instrumented with a sensor installed vertically so that the center of the sensing needles was located at a depth of approximately 5 cm. For visualization, sensor readings were averaged across the four instrumented pots, and daily mean, minimum, and maximum values were calculated.

2.3. Different time-scale gas monitoring experiments

2.3.1. Eight-month monitoring

N₂O and CO₂ fluxes were measured approximately every two weeks during plant growth (see 2.4 for gas measurement method). CO₂ fluxes were monitored together with N₂O fluxes to characterize plant carbon exchange during growth and residue decomposition after harvest. Following harvest, measurements were conducted more frequently (every 2–4 days) to capture rapid changes associated with nodule and residue decomposition. During the subsequent incubation period, measurements were generally conducted at weekly intervals, and the frequency was again increased to every 2–4 days after the drainage event.

2.3.2. Diurnal measurements

Diurnal measurements of CO₂, N₂O, and plant transpiration rate were conducted during plant growth period (16–27 January 2025; around flowering date) (see 2.5 for transpiration measurement method). The chamber light–dark cycle was shortened to approximately 22–23 h, which gradually shifted the timing of light transitions relative to the measurement schedule. As a result, measurements were obtained at four stages of the light–dark cycle: Day_end (1–3 h before lights-off), Night_start (1–4 h after lights-off), Night_end (1–3 h before lights-on), and Day_start (1–4 h after lights-on).

2.3.3. Light-off experiment

A light-off experiment was conducted during the plant growth period to examine short-term responses of N₂O, CO₂, and H₂O fluxes to the cessation of light. Measurements were conducted for Soramizuki on 17 January 2025 and Sachiutaka on 21 January 2025 (one pot each). Gas concentrations were continuously monitored before and after lights-off (for 30–60 minutes, depending on the measurements), and fluxes were calculated for successive 3-min intervals (see 2.4 for flux calculation method). Fluxes were subsequently aggregated into 10-min bins relative to the light-off event. Mean

fluxes and associated SE among the 3-min interval estimates within each bin were used for visualization. The first and last 3-min intervals of each measurement were excluded from the analysis.

2.4. Gas measurement and flux calculations

N₂O, CO₂, and H₂O concentrations were monitored using a Mira Pico gas analyzer (AERIS Technologies, Hayward, CA, USA). Sample air was circulated through a desiccating box containing silica gel and a Nafion tube before entering the analyzer to minimize interference from water vapor. The dehumidification system was based on a previously described design (Tokida, 2021). Measurements were conducted using a cylindrical acrylic chamber (radius 12.75 cm, height 50 cm) equipped with a 5-V fan to ensure air mixing during chamber closure. As plants grew, an open-top lower chamber was added to increase chamber height. Chamber closure periods ranged from approximately 4.5 to 24.5 min, with longer closure times used when concentration changes were small.

Gas fluxes were calculated from the temporal change in gas concentration during chamber closure. To avoid transient concentration changes associated with chamber placement and air mixing, fluxes were estimated from stable portions of the concentration time series. Concentration changes were fitted using robust linear regression, and fluxes were calculated from the resulting slope, chamber temperature, chamber volume, and soil surface area. Cumulative gas fluxes were calculated using linear interpolation between consecutive measurement dates and the trapezoidal integration method.

2.5. Transpiration measurements

Leaf-level transpiration was measured using a LI-600 porometer (LI-COR Biosciences, Lincoln, NE, USA) during the diurnal experiment. For each pot, one fully expanded leaf was selected from the upper, middle, and lower canopy, and transpiration rates were measured sequentially. The average of the three measurements was used as a representative index of plant transpiration. Measurements were conducted at the four stages of the light–dark cycle described above.

2.6. Biomass and yield measurements

Aboveground biomass was harvested on 14 April 2025, air-dried at room temperature for more than three months, and weighed. Seeds were subsequently separated from the dried plant material and weighed to determine seed yield.

2.7. Statistical analyses

All statistical analyses were conducted using R (version 4.5.2; R Core Team, Vienna, Austria). Differences among cultivars in aboveground biomass, seed yield, and cumulative gas fluxes were evaluated using linear models, followed by pairwise comparisons based on estimated marginal means with Tukey adjustment. Temporal patterns of CO₂ and N₂O fluxes were analyzed separately for each experimental phase using linear models with cultivar as a fixed effect and measurement date modeled using a common natural cubic spline ($df = 3$; `ns` function in the R `splines` package). Estimated marginal means were calculated for each experimental phase, and pairwise comparisons among cultivars were

performed using Tukey adjustment. Diurnal variation in N₂O flux was analyzed using linear mixed-effects models, with transpiration and soil temperature as fixed effects and cultivar as a random effect. Statistical significance was determined at $P < 0.05$.

3. Results

3.1. Aboveground biomass and yield

The cultivars developed as high-yield cultivars (Sorahibiki and Soramizuki) produced greater aboveground biomass and seed yield than the standard cultivars (Enrei and Sachiyutaka) (Fig. 1). Aboveground biomass was significantly greater in the high-yield cultivars than in the standard cultivars, whereas no significant differences were detected between Sorahibiki and Soramizuki or between Enrei and Sachiyutaka. Seed yield showed a similar pattern; however, the difference between Soramizuki and the standard cultivars was not statistically significant.

3.2. Temporal changes in CO₂ and N₂O flux over eight months

Temporal patterns of CO₂ and N₂O flux changed markedly throughout the eight-month experiment, despite relatively stable soil moisture conditions before drainage (Fig. 2). Soil volumetric water content remained at approximately 0.3 m³ m⁻³, indicating constantly near-saturated conditions based on the soil water retention relationship (Figs. 2a and S1). During the plant growth period (Phase 1), CO₂ flux was strongly negative, indicating net CO₂ uptake, and its magnitude gradually diminished as plants matured. In contrast, N₂O flux remained low and positive with little temporal variability during the growth period. After harvest (Phase 2), both gases increased, but their temporal trajectories diverged markedly. CO₂ flux increased within approximately two weeks after harvest and subsequently declined gradually. In contrast, N₂O exhibited a small transient peak within three days after harvest, followed by a sustained increase that continued for more than three months, even while CO₂ flux was already decreasing. Following drainage (Phase 3), CO₂ flux showed a slight increase and then gradually declined, whereas N₂O flux exhibited a brief decrease immediately after drainage, followed by a secondary increase and a subsequent sharp decline.

The overall temporal patterns of both CO₂ and N₂O fluxes were broadly consistent among cultivars; however, cultivar differences were observed for CO₂ during Phases 1 and 2 and for N₂O during Phase 2. The high-yield cultivars (Sorahibiki and Soramizuki) exhibited greater cumulative CO₂ uptake during Phase 1 than the standard cultivars (Enrei and Sachiyutaka) ($P < 0.01–0.05$; Fig. 3a). In addition, spline-based analysis of the temporal flux patterns revealed higher CO₂ emissions from the high-yield cultivars during Phase 2 ($P < 0.001$; Table 1). In contrast, cumulative N₂O emissions did not differ significantly among cultivars in any phase, although Soramizuki tended to exhibit lower cumulative emissions during

Phase 2 (Fig. 3). When temporal trends were accounted for using natural spline models, Soramizuki exhibited significantly lower N₂O fluxes than Sorahibiki during Phase 2 (Table 1).

Table 1
Estimated marginal means of CO₂ and N₂O fluxes during three experimental phases after accounting for temporal variation using natural spline models. Different letters indicate significant differences among cultivars within a phase (Tukey-adjusted comparisons, $P < 0.05$).

Variety	Phase 1	Phase 2	Phase 3
CO ₂ (g C m ⁻² h ⁻¹)			
Enrei	-0.58 a	0.12 c	0.09 a
Sachiyutaka	-0.64 a	0.12 c	0.09 a
Sorahibiki	-0.89 b	0.15 b	0.09 a
Soramizuki	-0.92 b	0.16 a	0.09 a
N ₂ O (μg N m ⁻² h ⁻¹)			
Enrei	2.0 a	11.4 ab	30.0 a
Sachiyutaka	3.2 a	11.6 ab	29.4 a
Sorahibiki	1.7 a	14.3 a	25.8 a
Soramizuki	2.4 a	9.3 b	26.3 a

3.3. Diurnal differences in CO₂ and N₂O flux

N₂O fluxes, CO₂ uptake, transpiration, and soil temperature were highest at Day_end and generally lower during the nighttime period (Fig. 4). N₂O fluxes at Night_start were approximately half of those observed at Day_end (Fig. 4d). An additional daytime measurement conducted nine days after the diurnal measurement period showed N₂O fluxes comparable to those observed at Day_end ($3.2 \pm 0.5 \mu\text{g N m}^{-2} \text{ h}^{-1}$). Similar diurnal patterns were observed for transpiration and CO₂ uptake, both of which decreased markedly during the nighttime period (Fig. 4b, c).

A linear mixed-effects model with cultivar included as a random effect indicated that transpiration was positively associated with N₂O fluxes ($P = 0.052$), whereas soil temperature was not significantly related to N₂O fluxes ($P = 0.72$).

3.4. Short-term responses of CO₂ and N₂O flux to light-off

Light-off induced rapid responses in CO₂ and N₂O fluxes (Fig. 5). CO₂ flux increased immediately after light-off. In contrast, N₂O flux declined more gradually but decreased by more than half within 20 minutes after light-off. During this period, soil temperature changed by less than 0.4°C.

4. Discussion

Temporal dynamics of N₂O emissions were largely governed by plant activity and soil moisture conditions. N₂O emissions remained low during plant growth, likely because nitrogen availability was limited by soybean uptake (Fig. 2; Phase 1). In contrast, N₂O emissions increased markedly for more than three months after harvest, indicating that decomposing roots became an important source of N₂O (Fig. 2; Phase 2). A small emission peak observed three days after harvest may have originated from nodule senescence (Inaba et al., 2012; Uchida and Akiyama, 2013), but its contribution appeared minor compared with the subsequent residue-driven emissions. This is likely because nodulation was limited under persistently wet soil conditions (Maekawa et al., 2011). Following drainage, N₂O emissions rapidly declined, indicating that residue-derived N₂O production was highly sensitive to soil moisture conditions.

Contrary to our initial hypothesis, one of the high-productivity cultivars tended to exhibit lower N₂O emissions. Although cultivar differences in cumulative N₂O emissions were not significant, Soramizuki generally showed relatively low N₂O fluxes after harvest (Figs. 2, 3; Table 1). Our initial hypothesis implicitly assumed that greater biomass production would increase substrate availability for N₂O production through larger root-derived carbon and nitrogen inputs. However, this assumption may not hold when soil N availability is limited. In the present experiment, no N fertilizer was applied, and nodulation was likely restricted, suggesting that soil N availability became increasingly limited during plant growth. Soramizuki exhibited greater aboveground biomass (Fig. 1) and may therefore have depleted soil nitrogen more effectively during growth, thereby reducing residual nitrogen available for N₂O production after harvest. Soramizuki also showed higher CO₂ emissions after harvest, suggesting greater decomposition of root-derived residues. Under conditions of limited soil N availability, these additional carbon inputs may have further promoted microbial nitrogen immobilization (Vigil and Kissel, 1991), thereby reducing substrate availability for N₂O production. Although indirect, this interpretation is consistent with the observation that N₂O emissions began to increase as CO₂ emissions declined (Fig. 2), suggesting that carbon-rich residues initially stimulated microbial activity while temporarily limiting nitrogen availability for N₂O production. In contrast to Soramizuki, Sorahibiki exhibited the highest fitted N₂O fluxes during Phase 2, but cumulative N₂O emissions remained comparable to those of the standard cultivars (Figs. 2 and 3; Table 1). These findings demonstrate that high productivity does not necessarily lead to greater N₂O emissions under nitrogen-limited conditions.

Cultivar differences were not detected during the growth period, probably because N₂O emissions were too low to resolve cultivar differences under nitrogen-limited conditions (Fig. 2, 3, Table 1). Despite the absence of detectable cultivar differences, soybean physiological activity appeared to influence N₂O

emissions during plant growth. Soil temperature is generally considered an important driver of diurnal variation in N₂O emissions through its effects on microbial activity (Alves et al., 2012). However, several lines of evidence in the present study suggest an important role of transpiration: the linear mixed-effects model indicated a stronger association of N₂O fluxes with transpiration than with soil temperature, and decreases in N₂O fluxes from Day_end to Night_start and following light-off coincided with decreases in transpiration or water vapor, while soil temperature changed only marginally (Figs. 4, 5, and S2). These results support an important role of plant-mediated processes in N₂O emissions, consistent with previous findings in other cropped systems (Chang et al., 1998; Zou et al., 2005). Therefore, under non-nitrogen-limited conditions, variation in aboveground biomass and whole-plant transpiration may contribute more strongly to cultivar differences in N₂O emissions.

The standardized, persistently wet, nitrogen-limited conditions in a controlled-environment chamber allowed cultivar differences in N₂O emissions to be evaluated while minimizing environmental variability. However, as with any controlled pot experiment, these conditions limited inorganic nitrogen availability and potentially constrained N₂O production pathways. Consequently, the cultivar differences observed in this study should not be directly extrapolated to field conditions. Similar conditions may occasionally occur in poorly drained soybean fields or rice–soybean rotation systems. However, under fertilized conditions, greater nitrogen availability may enhance N₂O production during plant growth. Under such conditions, high-productivity cultivars may show larger N₂O emissions because of their larger whole-plant transpiration. Likewise, under drier conditions where nodulation is less restricted, cultivar differences in nodule formation may contribute more strongly to N₂O emissions. Nevertheless, by minimizing the confounding effects of environmental variability, the present study provides mechanistic insight into cultivar differences in N₂O emissions from soybean cultivation.

Declarations

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

This study was supported by JSPS KAKENHI Grant Number 25K09388 and Cross-ministerial Strategic Innovation Promotion Program (SIP), "Building a Resilient and Nourishing Food Supply Chain Management for a Sustainable Future" (Grant Number JPJ012287; funding agency: Bio-oriented Technology Research Advancement Institution).

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Figures

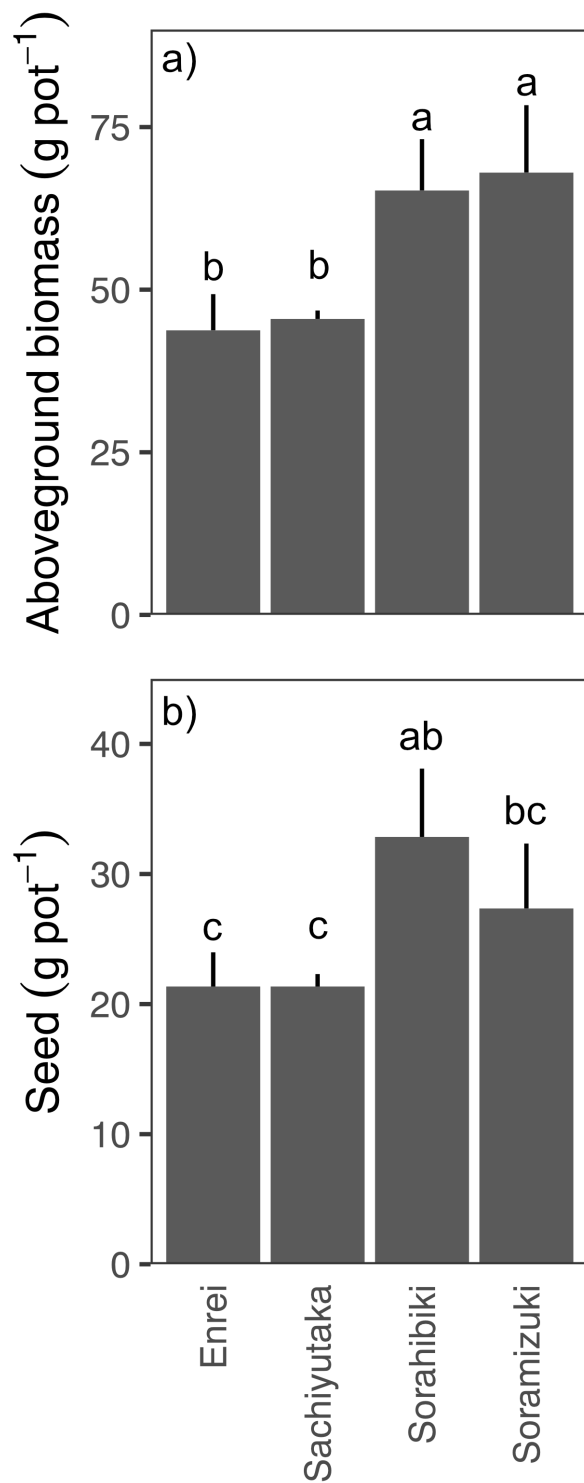


Figure 1

Aboveground biomass and seed yield of four soybean cultivars. Bars indicate means $\pm$ SD ($n = 4$). Different letters indicate significant differences among cultivars (Tukey's HSD test, $P < 0.05$).

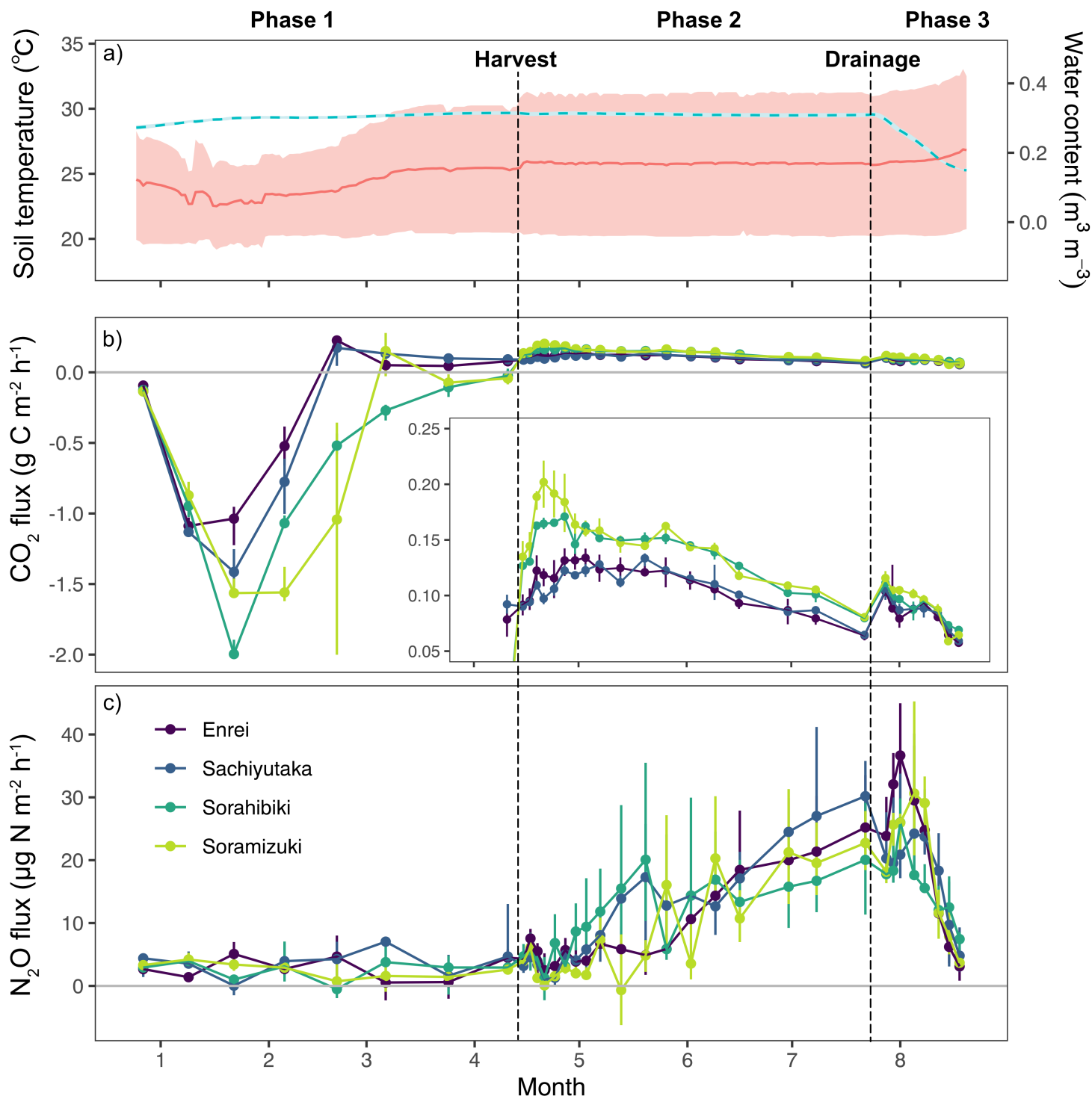


Figure 2

Temporal changes in soil temperature and water content (a), CO₂ flux (b), and N₂O flux (c) in pots cultivated with four soybean cultivars. Phases 1, 2, and 3 represent the plant growth, post-harvest wet, and post-drainage periods, respectively. Vertical dashed lines indicate harvest and drainage events. Lines and shaded areas in panel (a) represent daily mean values and daily minimum–maximum ranges, respectively, for soil temperature (solid line) and volumetric water content (dashed line). Symbols and

error bars in panels (b) and (c) represent median values and interquartile ranges (Q1–Q3), respectively. The inset in panel (b) shows an enlarged view of CO₂ fluxes after harvest.

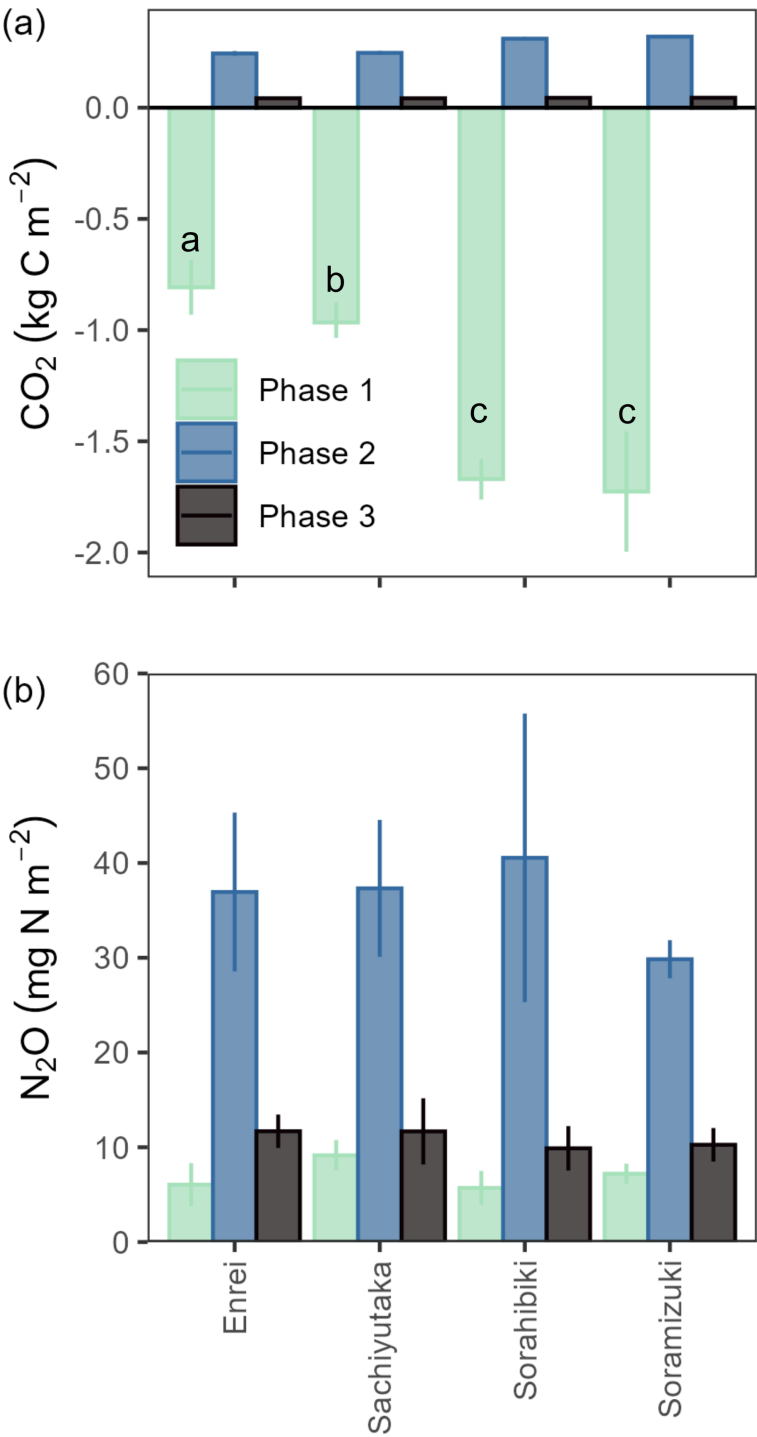


Figure 3

Cumulative CO₂ (a) and N₂O fluxes (b) during three experimental phases for four soybean cultivars (Phase 1: plant growth period under wet conditions; Phase 2: post-harvest period under wet conditions;

Phase 3: post-drainage period). Bars indicate means $\pm$ SE ($n = 4$). Different letters indicate significant differences among cultivars within a phase (Tukey's HSD test, $P < 0.05$). Negative CO_2 values indicate net CO_2 uptake.

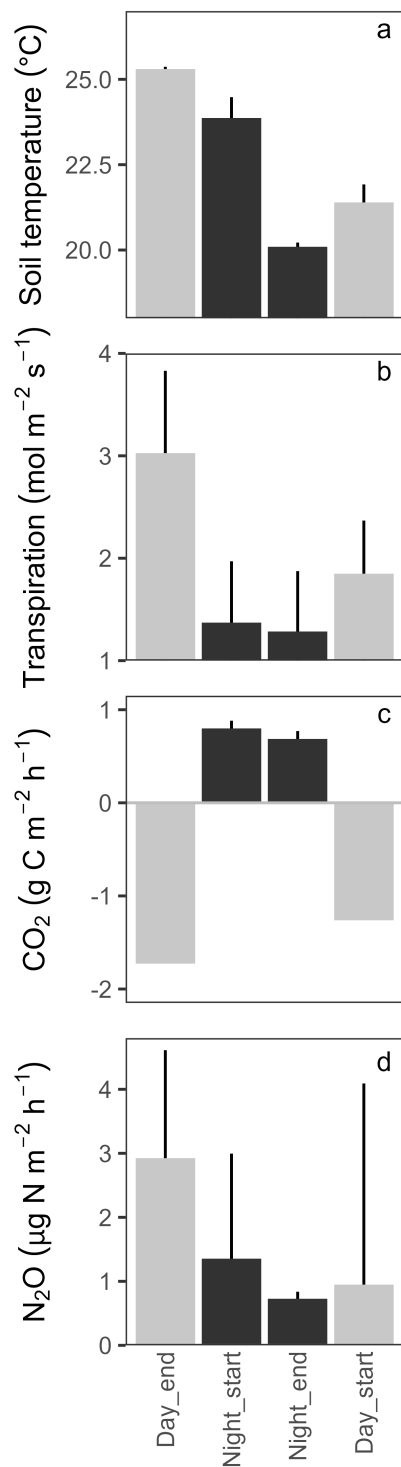


Figure 4

Diurnal variation in soil temperature (a), transpiration rate (b), CO₂ flux (c), and N₂O flux (d) during soybean growth. Measurements were conducted at the end of the daytime period (Day_end), at the beginning and end of the nighttime period (Night_start and Night_end), and at the beginning of the following daytime period (Day_start). Bars indicate means $\pm$ SD of cultivar median values ($n = 4$ cultivars).

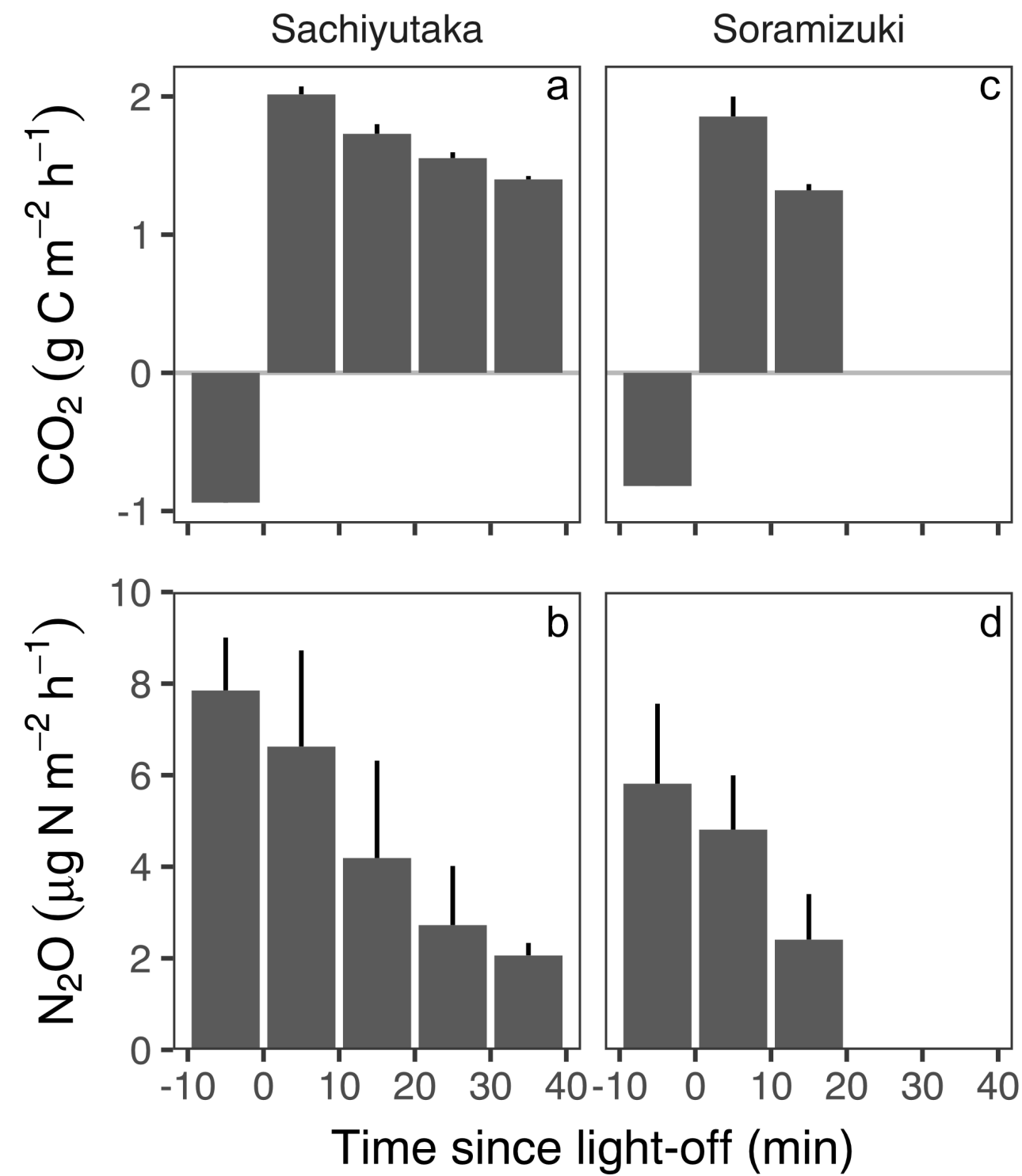


Figure 5

Short-term responses of CO₂ and N₂O fluxes to light-off in Sachiyutaka (a, b) and Soramizuki (c, d). CO₂ fluxes are shown in panels (a) and (c), and N₂O fluxes in panels (b) and (d). Time 0 indicates the light-off event. Bars represent mean fluxes calculated for 10-min intervals, and error bars indicate SE. Negative CO₂ flux values indicate CO₂ uptake. Monitoring duration differed between cultivars and was shorter for Soramizuki.

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