

Root Development and Radial Oxygen Loss Are Associated with Reduced Methane Emission in the Low-Emitting Doubled-Haploid Rice Line Milyang 392 Compared with Its *indica* Parent 93-11

Yun-Ho Oh , Jaeyoung Jang , Eunhee Kim, Mihyun Cho and Jae-Hyeon Oh 

Supercomputing Center, National Institute of Agricultural Sciences, Rural Development Administration, Wanju 55365, Korea

* Correspondence: jhoh8288@korea.kr

These authors contributed equally to this work.

Abstract: Rice (*Oryza sativa* L.) paddies are among the largest anthropogenic sources of methane (CH₄), and developing low-emission cultivars is a key mitigation strategy. We compared the doubled-haploid line Milyang 392, derived from a cross between the *indica* cultivar 93-11 and the *japonica* line Milyang 352, with its *indica* parent 93-11 over two growing seasons (2022–2023) using 1/2000-a Wagner pots. Cumulative CH₄ emission from Milyang 392 was 41.5% lower than that of 93-11 (117.3 vs. 200.4 kg/ha after diel correction; 391 vs. 668 kg/ha uncorrected), while grain yield was slightly higher in Milyang 392 (65.5±1.8 vs. 58.0±1.5 g/pot) and 1,000-grain weight was greater (23.8 vs. 19.5 g). Root cross-sections showed that Milyang 392 formed a more organized, radially symmetric aerenchyma, and the iron(II) sulfide (FeS) oxidation assay revealed strong, localized staining along its root surfaces, consistent with higher radial oxygen loss (ROL) at the root–rhizosphere interface. Because ROL was assessed qualitatively and only two contrasting genotypes were compared under pot conditions, these results should be interpreted as associations rather than direct causal evidence. Nevertheless, they suggest that well-developed root systems and localized rhizospheric oxygenation are candidate traits worth further quantitative and field-based validation for low-CH₄ rice breeding.

<https://doi.org/10.5338/KJEA.2026.45.13>

Agric. Environ. Sci. 2026, 45, 151-159

Received: June 29, 2026

Revised: July 24, 2026

Accepted: July 31, 2026

Published: August 19, 2026

Online ISSN: 2233-4173

Print ISSN: 1225-3537



Check for updates

© The Korean Society of Environmental Agriculture 2026



This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<https://creativecommons.org/licenses/by-nc/3.0/>) which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited.

Keywords: Aerenchyma, Methane emission, Milyang 392, Radial oxygen loss, Rice

Introduction

Rice paddies account for roughly one-tenth of global anthropogenic CH₄ emissions [1]. In continuously flooded soils, organic substrates are decomposed under anaerobic conditions by methanogenic archaea, and the resulting CH₄ is transported to the atmosphere primarily through the well-developed aerenchyma of the rice plant [2,3]. At the same time, oxygen (O₂) transported from shoots to roots can diffuse into the rhizosphere via radial oxygen loss (ROL) [4], sustaining aerobic methanotrophs that oxidize a substantial fraction of the locally produced CH₄ before it escapes to the atmosphere [5-7] (Fig. 1). The net emission is therefore determined by the balance between CH₄ production and the extent of rhizospheric oxidation, both of which are closely linked to root morphology. Both transgenic

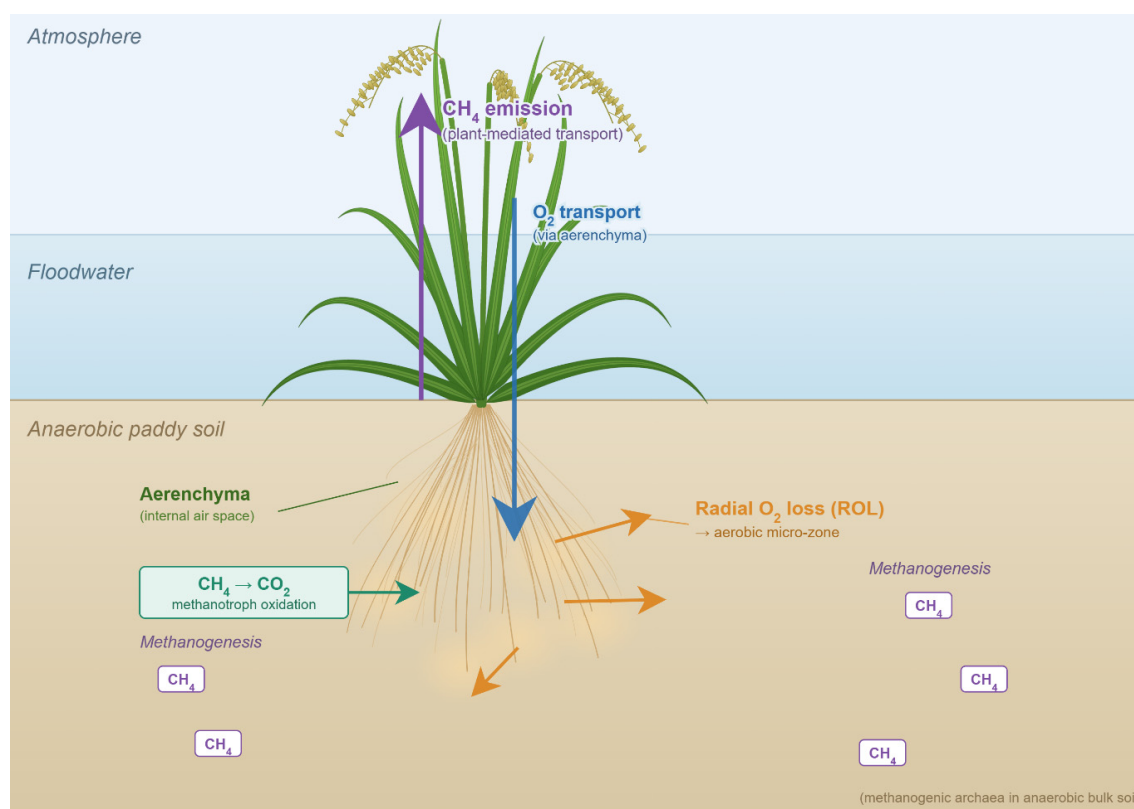


Fig. 1. Conceptual diagram of CH₄ production and radial oxygen loss (ROL) at the rice root–rhizosphere interface. CH₄ produced by methanogens in anoxic paddy soil is transported to the atmosphere primarily through the aerenchyma of the rice plant, while O₂ diffusing radially from roots sustains methanotrophs that oxidize a portion of the locally produced CH₄ before it escapes.

manipulation of carbon allocation and conventional screening of low-emitting cultivars have been explored as mitigation routes [8,9].

Milyang 392 is a doubled-haploid line derived from a cross between the high-yielding *indica* cultivar 93-11 and the *japonica* line Milyang 352 [10,11], and it was selected on the basis of preliminary indications of reduced CH₄ emission relative to its *indica* parent. The physiological basis of this low-emission phenotype, however, has not been characterized in detail. In this study, we quantified seasonal CH₄ emission, agronomic performance, root anatomical structure, and root-surface oxygenation in Milyang 392 and 93-11 grown over two consecutive seasons, in order to test whether root development and ROL-related traits are consistently associated with reduced CH₄ emission in this genetic background.

Results and Discussion

Seasonal CH₄ emission pattern and cumulative emission

Weekly CH₄ emission followed the typical bell-shaped seasonal course in both cultivars, rising after transplanting, peaking around the tillering-to-panicle-initiation window, and declining after midseason drainage (Fig. 2A). Peak weekly fluxes for 93-11 were consistently higher than those for Milyang 392 in both years. Diel-corrected cumulative seasonal emission averaged 200.4 kg/ha for 93-11 and 117.3 kg/ha for Milyang 392 across the two seasons, corresponding to a 41.5% reduction (Fig. 2B; Table 1). The corresponding uncorrected cumulative values were 668 and 391 kg/ha, respectively. The mixed-effects analysis showed a strong genotype effect ($p < 0.001$) and no significant genotype $\times$ year interaction, indicating that the genotype contrast was consistent across the two seasons; year alone contributed a modest amount of variation that is fully reflected in the year-specific

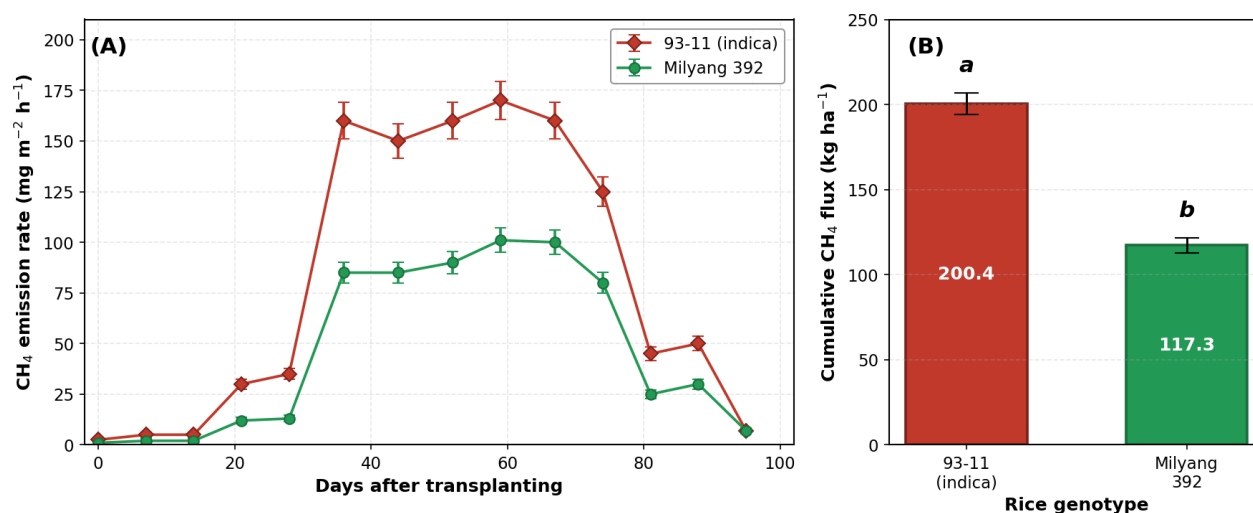


Fig. 2. (A) Weekly CH₄ flux (mg/m²/h) and (B) diel-corrected and uncorrected cumulative CH₄ emission (kg/ha) of 93-11 and Milyang 392 in 2022 and 2023. Bars are means±SE (n=6 pots/cultivar/year); individual pot values are overlaid.

Table 1. Cumulative CH₄ emission, heading date, and yield-related traits of 93-11 and Milyang 392 in 2022 and 2023 (mean±SE, n=6 pots/cultivar/year)

Trait	93-11 (2022)	93-11 (2023)	Milyang 392 (2022)	Milyang 392 (2023)
Heading date (DAT)	82	85	86	89
Cumulative CH ₄ emission (kg/ha, corrected)	204.6±8.1	196.2±7.3	119.8±5.2	114.8±4.7
Cumulative CH ₄ emission (kg/ha, uncorrected)	682±27	654±24	399±17	383±16
Panicles/plant	12.4±0.4	12.2±0.5	10.3±0.4	10.1±0.4
No. of spikelets/panicle	104.1±2.9	103.5±3.1	106.2±3.0	105.0±2.8
1,000-grain weight (g)	19.6±0.3	19.4±0.3	23.9±0.4	23.7±0.4
Grain yield (g/pot)	58.4±1.6	57.6±1.5	66.0±1.9	65.0±1.8

DAT=days after transplanting.

Values are pot-level means±SE (n=6 pots/cultivar/year). Grain yield is reported as dry grain mass per pot at 14% moisture content. Units follow the journal style (kg/ha, g/pot).

values in Table 1.

The absolute uncorrected fluxes exceed values typically reported for Korean paddies [17], which is expected for small Wagner pots with restricted lateral gas diffusion and continuous flooding. Because the same experimental system and the same diel correction were applied to both cultivars, the absolute values should be interpreted with caution, whereas the relative genotype contrast (−41.5%) is robust to the choice of correction. Multi-environment field validation will be needed before the absolute magnitude of the low-emission phenotype can be extrapolated to commercial paddy conditions.

Agronomic traits and grain yield

Milyang 392 headed 3–5 days later than 93-11 in both years (year-specific heading dates given in Table 1). Panicles per plant were slightly lower in Milyang 392 (10.2 vs. 12.3), whereas spikelets per panicle were similar (105.6 vs. 103.8). 1,000-grain weight was substantially higher in Milyang 392 (23.8 vs. 19.5 g), and grain yield was ~13% higher in Milyang 392 (65.5±1.8 vs. 58.0±1.5 g/pot; Table 1). Thus, the low-CH₄ phenotype of Milyang 392 was not associated with a yield penalty, at least under the present pot conditions.

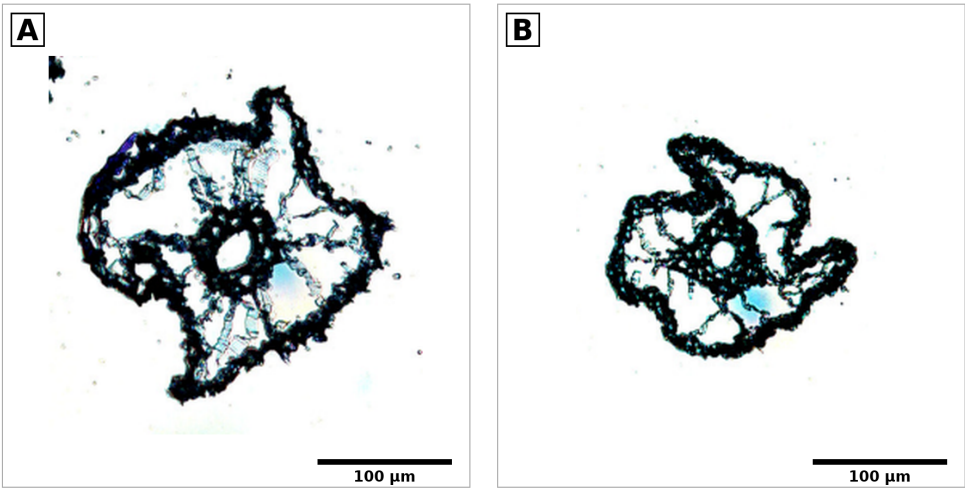


Fig. 3. Transverse sections of nodal roots (bright-field light micrographs) at the heading stage. (A) 93-11: lysigenous aerenchyma with less regular arrangement. (B) Milyang 392: more organized, radially symmetric aerenchyma. Scale bar = 100 μm.

Table 2. ImageJ-based two-dimensional root-area descriptors for 93-11 and Milyang 392 at the heading stage (2023)

Cultivar	Replicate	%Area	Mean particle area (mm ²)
93-11	Pot A	15.8	0.041
	Pot B	23.0	0.045
	Pot C	19.4	0.039
	Mean±SE	19.4±2.1	0.042±0.002
Milyang 392	Pot A	17.1	0.058
	Pot B	25.7	0.056
	Pot C	21.4	0.062
	Mean±SE	21.4±2.5	0.059±0.002

Replicate identifies the pot from which the scanned root system was taken (one root system per pot). %Area is the proportion of the two-dimensional scan area occupied by root structures, quantified with the Color Threshold and Analyze Particles functions of ImageJ. Mean particle area is the mean area of the disconnected root segments identified by the threshold. Data are from three independent pots per cultivar collected in 2023. Welch’s t-test indicated no statistically significant difference in mean %Area between cultivars ($t(3.9)=0.62$, $p=0.57$), but Milyang 392 tended to show higher %Area and larger mean particle area, consistent with more developed individual root structures. Given the small sample size, these results are treated as exploratory descriptors rather than definitive root-trait differences.

Root anatomy and ImageJ-based root-area descriptors

Transverse root sections from 93-11 showed lysigenous aerenchyma with a less regular arrangement, whereas Milyang 392 developed a more organized, radially symmetric aerenchyma with clearly delineated cortical airspaces (Fig. 3) [18,19]. At the whole-root scale, mean %Area was higher in Milyang 392 and mean per-particle area was ~1.4× that of 93-11 (Table 2), but the difference in %Area was not statistically significant (Welch’s t-test, $t(3.9)=0.62$, $p=0.57$), and the sample size ($n=3$ root systems per cultivar in 2023) limits the statistical power of this comparison. We therefore treat the ImageJ metrics as exploratory descriptors consistent with, but not proving, more developed individual root structures in Milyang 392. Broader biological replication would be needed to test the root-morphology contrast rigorously.

Root-surface oxygenation (FeS oxidation assay)

In the FeS oxidation assay, Milyang 392 showed strong, localized oxidation along the length of its seminal and nodal roots, whereas 93-11 showed weaker and more diffuse oxidation (Fig. 4). This pattern is consistent with more spatially organized rhizo-

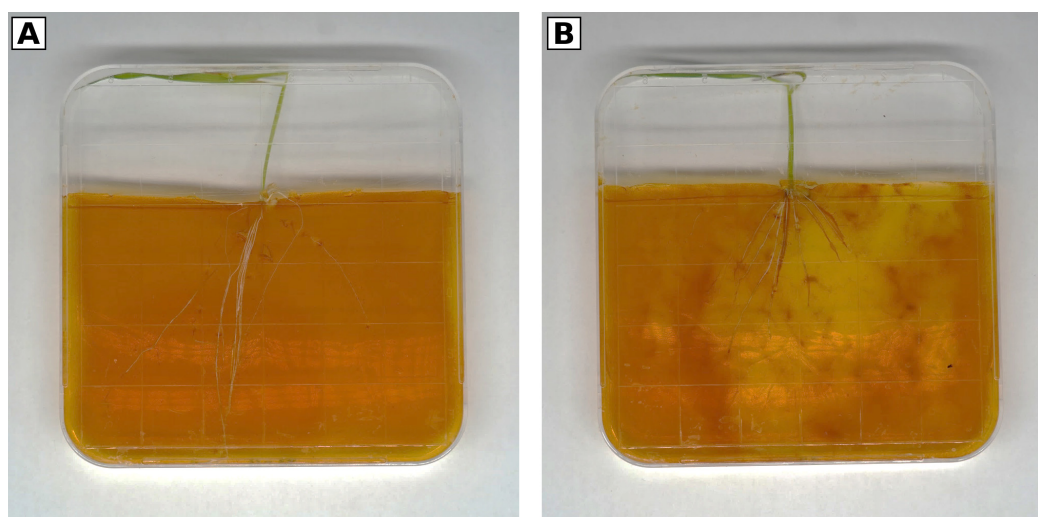


Fig. 4. FeS oxidation assay of 14-day-old seedlings. (A) 93-11; (B) Milyang 392. Localized oxidation of the FeS medium along the roots is more pronounced in Milyang 392 (B) than in 93-11 (A), a pattern consistent with stronger localized rhizospheric oxygenation. Panels are unretouched colour photographs shown at the same scale, with an identical brightness adjustment applied to both for visualization; no other image processing was performed.

spheric O₂ release in Milyang 392 [20]. However, because the assay is a qualitative, seedling-stage indicator, it does not by itself prove higher ROL activity in mature plants; we therefore describe the pattern as ‘consistent with higher ROL’ rather than as direct evidence. Quantitative validation at the adult stage using Clark-type oxygen microelectrodes is planned as the next step.

Genetic background and interpretation

Milyang 392 was derived from a 93-11 × Milyang 352 cross in which Milyang 352 served as the *japonica* donor of favorable root and physiological traits. The candidate high-ROL locus *qROL-2-1*, previously reported on chromosome 2 in a 93-11 × Milyang 352 doubled-haploid population [21], is a plausible contributor to the observed phenotype but was not directly genotyped or validated in the present study. Because only two contrasting genotypes were compared and other physiological factors (e.g., photosynthate partitioning to grain [22]) may also differ between the parents, the present data support an association between root traits, root oxygenation, and reduced CH₄ emission rather than a direct causal or genetic determination. Marker-assisted validation of *qROL-2-1* in a larger, genetically diverse panel will be required to strengthen the genetic interpretation.

Implications and limitations for breeding application

The ImageJ-based root-area analysis and the FeS oxidation assay used here are inexpensive and visually informative, but they were evaluated in only two contrasting genotypes under controlled pot conditions and are qualitative to semi-quantitative in nature. In their present form they should therefore be regarded as preliminary, candidate indicators that require further methodological development, higher-throughput adaptation, and multi-environment field validation before being used as routine screening tools in breeding programs. The findings are hypothesis-generating and encourage further exploration of root traits and rhizospheric oxygenation as complementary targets for low-CH₄ rice breeding.

Conclusions

Over two consecutive growing seasons, Milyang 392 emitted 41.5% less CH₄ than its *indica* parent 93-11 while producing slightly higher grain yield and heavier grains. The low-emission phenotype was associated with a more organized aerenchyma,

more developed individual root structures, and a root-surface staining pattern consistent with higher radial oxygen loss. Because the ROL assessment was qualitative and only two contrasting genotypes were compared under pot conditions, these results should be interpreted as evidence of association rather than as direct causal proof. The ImageJ-based root analysis and the FeS oxidation assay may serve as preliminary candidate indicators for low-CH₄ rice breeding once they are validated with quantitative ROL measurements (e.g., oxygen microelectrodes), marker-assisted validation of *qROL-2-1*, and multi-environment field trials.

Materials and Methods

Plant materials and growth conditions

The *indica* cultivar 93-11 and the doubled-haploid line Milyang 392 — derived from a 93-11 × Milyang 352 cross [10-12] — were grown in 1/2000-a Wagner pots (≈ 0.05 m² surface area, 5 L soil volume) in an outdoor pot facility at the National Institute of Agricultural Sciences (Wanju, Korea) during the 2022 and 2023 growing seasons. Three plants were transplanted per pot at 21 days after sowing, and pots were maintained under continuous flooding (~ 5 cm standing water) until 2 weeks before harvest, following standard paddy management. Basal fertilizer was applied at N-P₂O₅-K₂O = 90-45-57 kg/ha, with top-dressings applied at tillering and panicle initiation. Six pots per cultivar per year were grown to maturity for CH₄ monitoring and agronomic measurements. Transplanting dates, heading dates, harvest dates, soil properties, and daily meteorological summaries for each season are given in Supplementary Table S1.

Methane flux measurement and cumulative emission

CH₄ fluxes were measured weekly using a closed static chamber system [13] (chamber inner dimensions: 30 × 30 × 60 cm, headspace volume adjusted for plant height, sealed with a water-filled trough). Chambers were deployed once per week between 10:00 and 11:00 KST, and headspace gas was sampled at 0, 15, and 30 min after closure using 50-mL air-tight syringes. Samples were analyzed by gas chromatography (Agilent 7890B; FID at 250°C; Porapak Q column at 70°C; N₂ carrier at 25 mL/min). Instrument calibration was performed daily with certified 2 and 10 μ L/L CH₄ standards. Fluxes with linear-fit $R^2 < 0.90$ were discarded (<3% of all measurements).

Because the 10:00–11:00 window is close to the diurnal peak of CH₄ emission in flooded rice systems, weekly point fluxes were converted to representative daily means using a site-specific diel correction factor of 0.30 [14]. This factor was derived from pilot 24-h continuous chamber monitoring at the same experimental facility, in which the mean of eight three-hourly measurements over 24 h was compared with the 10:00–11:00 flux for a subset of pots; the mean ratio (24-h mean / late-morning flux) was 0.30 ± 0.06 ($n=12$ diel cycles, mixed cultivars and growth stages). The value is consistent with previously reported diurnal amplitudes in irrigated paddy systems [13,14]. For transparency, both the uncorrected cumulative fluxes (i.e., assuming the late-morning flux is representative of the 24-h mean) and the diel-corrected values are reported (Fig. 2). Because the same correction factor was applied to both cultivars in each week, it affects the absolute cumulative estimates but not the genotype contrast, which is our primary inference target.

Agronomic traits and grain yield

At physiological maturity, all plants in each pot were harvested. Panicles per plant and spikelets per panicle were counted on all plants in each pot. Grain yield was determined as dry grain mass per pot (g/pot) after air-drying to 14% moisture content, and is reported on that basis throughout the manuscript. Filled grains were defined as grains sinking in tap water and with a 1,000-grain weight above 15 g; 1,000-grain weight was measured on filled grains at 14% moisture.

Root sampling, anatomy, and ImageJ-based analysis

At the heading stage, three additional pots per cultivar per year (separate from the six maturity pots) were destructively sampled. Root systems were carefully washed free of soil, spread on a transparent tray, and scanned at 600 dpi (Epson Expression 12000XL). Two-dimensional root-area coverage (%Area) and mean per-particle area were quantified in ImageJ (v1.53) [15] using a fixed color-threshold and the Analyze Particles function; the same threshold parameters were applied to all images. Quantitative root-area descriptors are reported here for the 2023 season (Table 2). Representative scanned root systems of the two genotypes at the heading stage are provided in Supplementary Fig. S1. Additional root segments (nodal roots at 5–10 cm from the base) were hand-sectioned and examined under bright-field light microscopy for aerenchyma observation. Because the ImageJ metrics are 2-D descriptors sensitive to washing and scanning conditions, they are used here as exploratory supporting information rather than as definitive quantitative root traits.

Radial oxygen loss (FeS oxidation assay)

Seedling-stage ROL was visualized by an iron(II) sulfide (FeS) oxidation assay, with the FeS-containing agar medium prepared as described previously [21]. Seeds were sown on the FeS medium (two seedlings per plate; three plates per cultivar), and plate images were taken at 14 days after sowing. The experimental unit was one plate. Localized oxidation of the medium along the root surface was interpreted as a qualitative, indirect indicator of oxygen release from roots [16]. We do not treat the staining pattern as a direct quantitative measure of ROL; rather, it is used to compare the spatial pattern of root-surface oxygenation between the two genotypes.

Statistical analysis

Weekly CH₄ fluxes were analyzed with a linear mixed-effects model in which genotype, sampling week, year, and their interactions were treated as fixed effects, and pot (nested within year) as a random effect, reflecting the repeated-measures structure of the weekly flux series. Seasonal cumulative CH₄ emissions and agronomic traits were analyzed with a two-way model including genotype, year, and genotype × year as fixed factors, with pot as the experimental unit. Year-specific values are also reported (Table 1, Fig. 2) so that interannual variation is fully visible. Standard errors reported for cumulative CH₄ and agronomic traits reflect pot-level replication within each year (n=6 pots/cultivar/year). Where only two genotypes are compared, individual pot observations are shown alongside the mean rather than significance letters. Analyses were performed in R (v4.3) using the lme4 and lmerTest packages; a two-sided α of 0.05 was used throughout.

Data Availability: All data are available in the main text or in the Supplementary Information.

Author Contributions: Conceptualization: J.H.O.; Methodology and Investigation: Y.H.O., J.J., E.K., M.C.; Formal analysis and Visualization: Y.H.O., J.J.; Data curation: E.K., M.C.; Writing—original draft: Y.H.O., J.J.; Writing—review and editing: J.H.O.; Supervision and Funding acquisition: J.H.O.

Notes: The authors declare no conflict of interest.

Acknowledgments: This work was supported by a grant from the National Institute of Agricultural Sciences Program (Project No. RS-2022-RD010034), Rural Development Administration, Republic of Korea. The authors declare no conflicts of interest. AI tools (large language models) were used exclusively for English-language editing and were not used for experimental design, data analysis, or scientific conclusions. All scientific content was generated and verified by the authors.

Additional Information:

Supplementary information The online version contains supplementary material available at <https://doi.org/10.5338/KJEA.2026.45.13>

Correspondence and requests for materials should be addressed to Jae-Hyeon Oh.

Peer review information Agricultural and Environmental Sciences thanks the anonymous reviewers for their contribution to the peer review of this work.

Reprints and permissions information is available at <http://www.korseaj.org>

References

1. Conrad R (2002) Control of microbial methane production in wetland rice fields. *Nutrient Cycling in Agroecosystems*, 64, 59-69. <https://doi.org/10.1023/A:1021178713988>.
2. Nouchi I, Mariko S, Aoki K (1990) Mechanism of methane transport from the rhizosphere to the atmosphere through rice plants. *Plant Physiology*, 94, 59-66. <https://doi.org/10.1104/pp.94.1.59>.
3. Armstrong W (1979) Aeration in higher plants. *Advances in Botanical Research*, 7, 225-332. [https://doi.org/10.1016/S0065-2296\(08\)60089-0](https://doi.org/10.1016/S0065-2296(08)60089-0).
4. Visser EJW, Colmer TD, Blom CWPM, Voesenek LACJ (2000) Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. *Plant, Cell & Environment*, 23, 1237-1245. <https://doi.org/10.1046/j.1365-3040.2000.00628.x>.
5. Bodelier PLE, Roslev P, Henckel T, Frenzel P (2000) Stimulation by ammonium-based fertilizers of methane oxidation in soil around rice roots. *Nature*, 403, 421-424. <https://doi.org/10.1038/35000193>.
6. Le Mer J, Roger P (2001) Production, oxidation, emission and consumption of methane by soils: a review. *European Journal of Soil Biology*, 37, 25-50. [https://doi.org/10.1016/S1164-5563\(01\)01067-6](https://doi.org/10.1016/S1164-5563(01)01067-6).
7. Watanabe A, Takeda T, Kimura M (1999) Evaluation of origins of CH₄ carbon emitted from rice paddies. *Journal of Geophysical Research: Atmospheres*, 104, 23623-23629. <https://doi.org/10.1029/1999JD900467>.
8. Su J, Hu C, Yan X, Jin Y, Chen Z, Guan Q, Wang Y, Zhong D, Jansson C, et al. (2015) Expression of barley *SUSIBA2* transcription factor yields high-starch low-methane rice. *Nature*, 523, 602-606. <https://doi.org/10.1038/nature14673>.
9. Jiang Y, van Groenigen KJ, Huang S, Hungate BA, van Kessel C, Hu S, Zhang J, Wu L, Yan X, et al. (2017) Higher yields and lower methane emissions with new rice cultivars. *Global Change Biology*, 23, 4728-4738. <https://doi.org/10.1111/gcb.13737>.
10. Han J, Lee SY, Jun Y, Lee SM, Eom GH, Lee JH, Mo Y (2025) Identification of QTL for rice panicle length and grain weight using a doubled haploid population derived from 93-11 and Milyang352. *Plant Biotechnology Reports*, 19, 123-135. <https://doi.org/10.1007/s11816-025-00962-4>.
11. Lee SM, Kang JW, Cho JH, Lee JY, Shin DJ, Kwon YH, Cha JK, Lee SB, Ko JM, et al. (2020) QTL analysis of heading date using 93-11 × Milyang352 doubled haploid lines in rice. *Korean Journal of Breeding Science*, 52, 332-341. <https://doi.org/10.9787/KJBS.2020.52.4.332>.
12. Kwon YH, Kabange NR, Lee JY, Lee SM, Cha JK, Shin DJ, Cho JH, Kang JW, Ko JM, et al. (2021) Novel QTL associated with shoot branching identified in doubled haploid rice (*Oryza sativa* L.) under low nitrogen cultivation. *Genes*, 12, 745. <https://doi.org/10.3390/genes12050745>.
13. Minamikawa K, Tokida T, Sudo S, Padre A, Yagi K (2015) Guidelines for measuring CH₄ and N₂O emissions from rice paddies by a manually operated closed chamber method. *National Institute for Agro-Environmental Sciences, Tsukuba, Japan*, 76 pp.
14. Minamikawa K, Yagi K, Tokida T, Sander BO, Wassmann R (2012) Appropriate frequency and time of day to measure methane emissions from an irrigated rice paddy in Japan using the manual closed chamber method. *Greenhouse Gas Measurement and Management*, 2, 118-128. <https://doi.org/10.1080/20430779.2012.729988>.
15. Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671-675. <https://doi.org/10.1038/nmeth.2089>.
16. Kludze HK, DeLaune RD, Patrick WH Jr (1993) Aerenchyma formation and methane and oxygen exchange in rice. *Soil Science Society of America Journal*, 57, 386-391. <https://doi.org/10.2136/sssaj1993.03615995005700020017x>.
17. Kwon Y, Lee JY, Choi J, Lee SM, Kim D, Cha JK, Park H, Kang JW, Kim TH, et al. (2023) Loss-of-function *gs3* allele decreases methane emissions and increases grain yield in rice. *Nature Climate Change*, 13, 1329-1333. <https://doi.org/10.1038/s41558-023-01872-5>.
18. Uga Y, Sugimoto K, Ogawa S, Rane J, Ishitani M, Hara N, Kitomi Y, Inukai Y, Ono K, et al. (2013) Control of root system architecture by *DEEPER ROOTING 1* increases rice yield under drought conditions. *Nature Genetics*, 45, 1097-1102. <https://doi.org/10.1038/ng.2725>.
19. Colmer TD (2003) Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant, Cell & Environment*, 26, 17-36. <https://doi.org/10.1046/j.1365-3040.2003.00846.x>.
20. Zheng H, Fu Z, Zhong J, Long W (2018) Low methane emission in rice cultivars with high radial oxygen loss. *Plant and Soil*, 431,

- 119-128. <https://doi.org/10.1007/s11104-018-3747-x>.
21. Duyen DV, Kwon Y, Kabange NR, Lee JY, Lee SM, Kang JW, Park H, Cha JK, Cho JH, et al. (2022) Novel QTL associated with aerenchyma-mediated radial oxygen loss (ROL) in rice (*Oryza sativa* L.) under iron (II) sulfide. *Plants*, 11, 788. <https://doi.org/10.3390/plants11060788>.
22. Denier van der Gon HAC, Kropff MJ, van Breemen N, Wassmann R, Lantin RS, Aduna E, Corton TM, van Laar HH (2002) Optimizing grain yields reduces CH₄ emissions from rice paddy fields. *Proceedings of the National Academy of Sciences USA*, 99, 12021-12024. <https://doi.org/10.1073/pnas.192276599>.

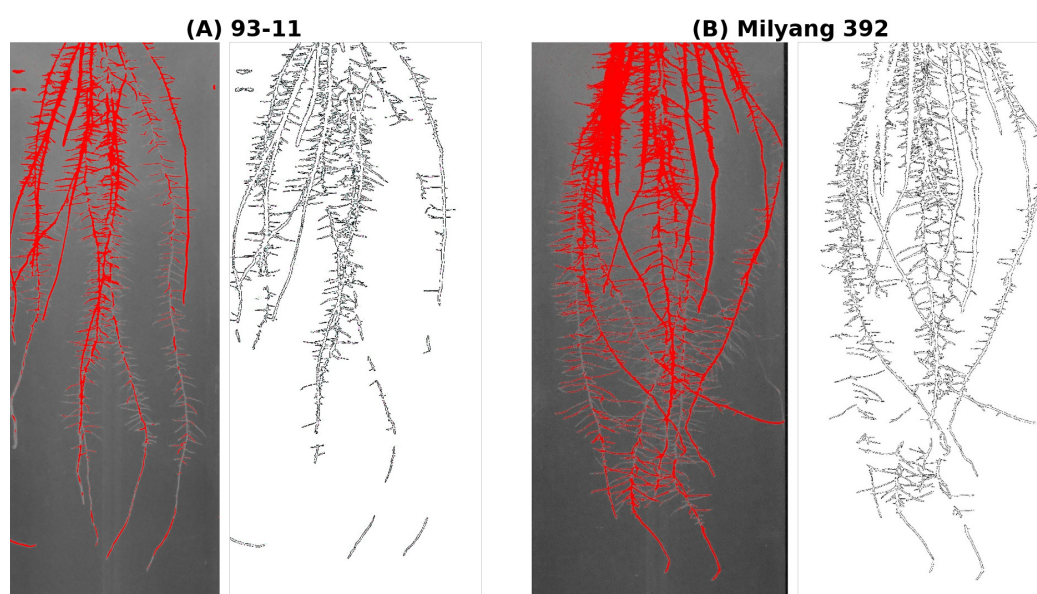


Fig. S1. Representative root systems of (A) 93-11 and (B) Milyang 392 at the heading stage, with two individuals shown per genotype. Whole root systems were washed free of soil, spread on a transparent tray, and scanned; these images correspond to the exploratory ImageJ-based two-dimensional root-area analysis summarized in Table 2. Milyang 392 tended to show more extensive lateral branching and greater root-area coverage than 93-11.