

Physiological functions and methane and oxygen exchange in Korean rice cultivars grown under controlled soil redox potential

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(Received April 17, 1998; Accepted January 6, 1999)

Abstract. Two Korean rice varieties (*Oryza sativa* L., cv. Nonganbyeo and Dongjinbyeo) were grown under laboratory conditions in Crowley silt loam (fine, montmorillonitic, thermic fluvaquent) soil suspension maintained at different redox potential (Eh) levels (-150, +150 and +350 mV). Plant growth, aerenchyma formation, radial oxygen loss, net CO₂ assimilation, CH₄ production (soil) and emission were measured. In general, plant height, root length, dry weight and carbon fixation for Nonganbyeo decreased under strongly reduced conditions (-150 mV). For Dongjinbyeo only a decrease in CO₂ fixation was observed at -150 mV as compared to moderately reduced conditions (+150 mV and +350 mV). Under strongly reduced conditions (-150 mV) root porosity was less than rice grown at the two higher redox levels. Since greatest soil methane production occurred under strongly reduced conditions (-150 mV) no emission from the two rice cultivars were measured under moderately reduced soil conditions. However, under the strongly reduced soil conditions where methane was formed, there were apparent differences in methane emission between the two varieties studied. Methane production in pot in which DJB was grown was approximately 50 times greater than that of NAB but net emission was only greater by the factor of 3. Net carbon assimilation varied depending on soil Eh. Reduced soil conditions (Eh -150 mV) decreased net photosynthesis for both varieties. Radial oxygen loss on the other hand was greatest at Eh -150 mV, and this can be attributed to more oxygen demand under more reduced soil conditions. Results demonstrate that the degree of soil reduction influences both rice growth and methane emission. Management practices should consider growing the two rice cultivars under moderately reduced soil conditions where best carbon fixation was measured. Growth under these conditions would also reduce methane emission to atmosphere.

Keywords: Aerenchyma formation; Carbon dioxide fixation; Korea; Methane emission; *Oryza sativa*; Radial oxygen loss.

Abbreviations: DJB, Dongjinbyeo; Eh, redox potential; NAB, Nonganbyeo; NCA, net CO₂ assimilation, ROL, radial oxygen loss.

Introduction

Rice is vital to more than half of the world's population (Vlek and Byrnes, 1986). It is the most important food grain in the diet of hundred of millions of Asians, Africans, and Latin Americans living in the tropics and subtropics. Approximately 75~80% of cultivated rice is grown under rainfed or irrigated wetland conditions or under submerged paddy field conditions. This is done to increase grain yield (Lindau et al., 1993) or because biophysical conditions do not allow the growth of crops upland.

Soil redox potential can affect rice growth. Subsequent to flooding, plant roots encounter hypoxic and anoxic conditions as a result of the depletion of soil oxygen by microbial and plant root respiration (Gambrell and Patrick,

1978). Flooded soils can experience redox conditions ranging from well-oxidized to strongly reduced. In an oxidized (aerobic) soil the redox potential (Eh) ranges from about +600 to +350 mV, whereas in most reduced (anaerobic) soils the Eh varies from about -300 to +350 mV (DeLaune et al., 1990; Masscheleyn et al., 1993).

Methane gas is one of the greenhouse gases that is reported to exert significant effects on the global heat balance, thus causing a possible elevation of global surface temperature (Bouwman, 1991). Rice paddies can serve as CH₄ sources and sinks because soil conditions allow methane-generating and methane-oxidizing bacteria to exist in close approximation (Oremland and Culbertson, 1992). CH₄ emissions from paddy fields are highly variable and determined by complex interactions among the chemical, physiological, and biological properties of the local environment (Bartlett et al., 1985). Rice plants develop aerenchyma, which provides the roots with O₂ (Kludze et al., 1994). Thus, much higher CH₄ emissions were found in vegetated rice fields than in those that were not vegetated (Cicerone and Shetter, 1993).

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Root oxygenation is an important adaptation that helps flood-tolerant plants overcome anaerobic conditions (Armstrong, 1979; Grosse and Schroder, 1985). Thus, easy access of the rhizosphere to O₂ from the atmosphere via a well-developed aerenchyma system would enhance the oxidation of CH₄ gas in the rhizosphere and hence mitigate its flux into the atmosphere (Hanson, 1980). A positive relationship has been established between the intensity of soil anaerobiosis and both aerenchyma formation and radial oxygen loss (Kludze et al., 1993).

Even though variations in methane production and emission have been reported to depend on soil redox conditions in rice plants (Kludze and DeLaune, 1994), the production of CH₄ and CO₂ and its effects on the physiological functions and growth of Korean rice cultivars have not been investigated. Thus, this study was conducted to determine (i) biomass partitioning between root and shoot, (ii) CH₄ production and emission, (iii) CO₂ production and flux and photosynthetic responses, (iv) aerenchyma formation, and (v) radial oxygen loss (ROL) from plant roots in two agriculturally important Korean rice cultivars growing under controlled soil redox potentials ranging from slightly reduced (+350 mV) to strongly reduced (-150 mV).

Materials and Methods

Incubation of Soil Suspension

The substrate used in this study was a Louisiana paddy soil (Crowley silt loam) collected from the Rice Research Station at Crowley, Louisiana. The soil was air dried, ground, sieved through a 1-mm mesh screen, and thoroughly mixed before being used. The dry soil had a pH of 5.7 (1:1, soil/water), CEC of 9.4 cmol kg⁻¹, 110 g clay kg⁻¹, 710 g silt kg⁻¹, and total C and N contents of 7.0 g kg⁻¹ and 0.5 g kg⁻¹, respectively. Soil suspensions were prepared by mixing 400 g of the dry soil with 1,200 mL of deionized water. Two grams of finely ground rice straw were added to the soil to provide an extra energy source for microbial activity. The suspensions were equilibrated at 25±1°C under controlled Eh levels of -150, +150, and +350 mV in modified microcosms as described by Reddy et al. (1976).

Plant Materials

Seeds of short-grain type rice cultivars, Nonganbyeo (NAB) and Dongjinbyeo (DJB) were soaked in fungicide solution for 1 d, rinsed with tap water, and allowed to germinate and sprout in petri-dishes. The seeds were transferred to an aluminum nursery tray containing air dried sand with 10% Hoagland nutrient solution. Twenty-five days after germination, 10 healthy seedlings of equal size were transplanted into incubated soil suspensions (microcosms). Qubitac sealant (Qubit Systems Inc. Canada) was used to seal the plants in the Plexiglass plate cover. Plants were grown for a total of 60 d. Incubating and culturing processes were performed under the same laboratory conditions three times.

Methane Gas Production and Emission

Methane production at the various soil redox potentials was measured as described by Kludze et al. (1993). A series of soil suspension aliquots (6 mL) were withdrawn from each microcosm with a plastic syringe and dispensed into 10 mL evacuated vacutainers (Becton Dickinson, Lincoln park, NJ). The amount of CH₄ produced in the headspace was measured in triplicate hourly for 8 h. The rate of CH₄ production was determined by regression analysis of CH₄ accumulation as a function of time. The best linear fit was found in the period between 0 and 6 h. After sampling the gas, the vacutainers were dried at 100°C for 3 d, and the amounts of dry soil were determined.

A diffusion chamber method, as described by Minami and Yagi (1988), was used for measuring CH₄ flux from rice plants. Methane emission within a 60 d period was determined by measuring the temporal increase of CH₄ concentration in the air within the diffused chamber. The emission rates were measured under dark and light conditions. Gas samples in the chamber were collected using vacutainers at 0 and 30 min after placing either translucent or dark chambers over the plants.

The CH₄ concentrations of gas samples collected from the chambers in vacutainers were determined using a Shimadzu 14A gas chromatograph equipped with a flame ionized detector (Lindau et al., 1991). The production and flux rate of CH₄ from the soil suspension and rice plants were estimated using the modified equation of Rolston (1986) and expressed in mg of CH₄ pot⁻¹ d⁻¹.

Carbon Dioxide Fixation

A gaseous diffusion chamber (Smith et al., 1981) was used to quantify the relative photosynthetic CO₂ fixation as a plant growth indicator in response to treatments. The procedure involved placing light and dark chambers over the plants as previously described (Kludze and DeLaune, 1994). The dark chambers were constructed by completely covering the outer surface of the clear chambers with aluminum foil. The headspaces were sampled at 0 and 30 min after covering. A gas chromatograph (Shimadzu GC-14, Scientific Instruments, Columbia, MD), equipped with a thermal conductivity detector, was used to determine the CO₂ concentrations (in the headspace). Calculation of the rate of CO₂ fixation or respiration followed the method of Smith et al. (1981).

Changes in the CO₂ concentration within the light and dark chambers were considered to be estimates of net plant CO₂ fixation and photo respiration, respectively; gross CO₂ fixation was calculated from the algebraic sum of the emissions determined with the light and dark chambers. Net CO₂ fixation and respiration were measured at 35 d after transplanting (60 d old seedlings). All results reported are the average of three replications followed by standard deviation. Net CO₂ assimilation data were expressed as mg plant⁻¹ d⁻¹.

Measurement of Radial Oxygen Loss (ROL)

The rate of O₂ released through roots was estimated colorimetrically with Ti³⁺-citrate solution in 60 d (after germination) rice plants. This technique was described in detail by Kludze et al. (1993). The Ti³⁺-citrate solution was prepared under an N₂ atmosphere according to the method of Zehner and Wuhrman (1976). Three-hundred milliliters of deoxygenated water were added to 17.7 g of sodium citrate to give a final concentration of 0.2 M sodium citrate solution. Thirty milliliters of 1.16 M TiCl₃ (Aldrich Chemical Co., Milwaukee, WI) were then added to the sodium citrate solution, and the pH was adjusted to 5.6 by adding saturated Na₂CO₃. Forty milliliters of 10% Hoagland nutrient solution was poured into 50-mL test tubes, and He gas was bubbled through them for 30 min to remove any dissolved O₂. Plant samples were washed, coated with parafilm at the bases, and inserted into the tubes. Immediately after this, the solution surfaces were layered with 2 cm of paraffin oil (light natural oil, Fisher) to prevent atmospheric O₂ contamination. A 5 mL aliquot of Ti³⁺-citrate was then injected into each test tube with a syringe. Control treatments had no plants. Six hours after the introduction of roots into Ti³⁺-citrate solution, the test tubes were gently shaken, and the solution was sampled with a syringe through rubber tubing.

Measurements of the absorbance of the partly oxidized Ti³⁺-citrate solution were made at 527 nm using a Perkin-Elmer Lambda 3 UV/VIS spectrophotometer. Released O₂ was determined by extrapolation of the measured absorbance to a standard curve previously obtained from a dilution series of the Ti³⁺-citrate solution being used. Net rate of ROL was then calculated with the formula (Kludze et al., 1993):

$$\text{ROL} = c(y-z)$$

where ROL = radial oxygen loss ($\mu\text{mol O}_2 \text{ plant}^{-1} \text{ d}^{-1}$),

c = initial volume of Ti³⁺-citrate added to each test tube (L),

y = concentration of Ti³⁺-citrate solution of control (without plants) ($\mu\text{mol Ti}^{3+} \text{ L}^{-1}$),

z = concentration of Ti³⁺-citrate solution after 6 h with plants ($\mu\text{mol Ti}^{3+} \text{ L}^{-1}$).

Measurement of Root Porosity

Root porosity was measured by the pycnometer method (Jensen et al., 1969; Kludze et al., 1993). A 25-mL pyc-

nometer was filled with water and weighed. Approximately 0.2–0.3 g of fresh roots (2–2.5 cm below the collar) of 60 d old plants were gently blotted dry using tissue paper, introduced into the water-filled pycnometer, and reweighed. The roots were later retrieved, ground into a paste with mortar and pestle, and the resulting homogenate of the roots was returned to the pycnometer for reweighing. Root porosity was determined, using the formula (Kludze et al., 1993):

$$\text{POR} = \frac{[p\&gr] - (p\&r)}{[(r+p) - (p\&r)]} \times 100$$

where POR = root air space (porosity) (%),

r = mass of roots (g),

p = mass of water-filled pycnometer (g),

p&r = mass of pycnometer with roots and water (g),

p&gr = mass of pycnometer with ground roots and water (g).

Results and Discussion

Plant Growth

Under our experimental conditions (stirred soil suspension, not field conditions) DJB showed no effects of changing Eh whereas NAB had reduced plant height, root length, and shoot weight at -150 mV (Table 1). Both rice varieties showed that shoot and root weight was somewhat lower at Eh -150 mV than at Eh +150 mV. This result indicated that moderately reduced soil conditions were more favorable for root growth in rice plants than strongly reduced conditions (-150 mV).

Methane Gas Production and Emission

Significantly more methane was produced under extremely reduced conditions (-150 mV) in soil in which DJB was grown as compared to NAB (the only soil redox condition in which methane was produced). The amount of CH₄ produced in soil grown to DJB plants was approximately 50 times that of the soil grown to NAB (Table 2). At -150 mV, the pot grown to NAB did not produce more CH₄ than the unvegetated control (Table 2), suggesting that NAB did not stimulate methanogenesis, as opposed to DJB, which strongly enhanced it. The critical soil Eh for CH₄ production in soils was reported to be approximately -150 mV (Jugsujinda et al., 1995). Varietal differences in the root exudates associated with root growth were reported to control CH₄ production (Kludze et al.,

Table 1. Effect of soil redox potential (Eh) on root and shoot growth of rice cultivars after 60 days of soil incubation.

Cultivar	Eh (mV)	Plant ht. (cm)	Root length (cm)	Shoot wt. (mg)	Root wt. (mg)	Ratio shoot/Root wt.
Nonganbyeo	-150	37.5 ± 2.1	12.3 ± 0.5	205 ± 38	87 ± 11	2.3
	+150	43.0 ± 3.1	18.5 ± 1.0	302 ± 27	92 ± 25	3.2
	+350	45.5 ± 6.0	21.8 ± 1.2	308 ± 60	79 ± 19	3.9
Dongjinbyeo	-150	52.8 ± 6.5	18.8 ± 2.3	164 ± 12	74 ± 14	2.5
	+150	46.5 ± 4.7	21.3 ± 1.7	215 ± 43	94 ± 21	1.9
	+350	55.0 ± 3.5	18.0 ± 2.1	244 ± 44	64 ± 17	3.8

Data are means of three replications, ± values indicate standard deviation.

Table 2. Rate of methanogenesis, CH₄ emission and percentage of CH₄ emitted in laboratory culture of rice after 60 days of soil incubation.

Soil redox potential (Eh)	Cultivar	CH ₄ production (mg pot ⁻¹ d ⁻¹)	CH ₄ emission		CH ₄ emitted (%)	
			Light	Dark	Light	Dark
-150	Nongan	42 ± 12	16.1	(9.8)	39.0	(23.3)
	Dongjin	2254 ± 82	54.1	(45.1)	2.4	(2.0)
+150	Nongan	0 ± 00	0.0	(0.0)	0	(0)
	Dongjin	0 ± 00	0.0	(0.0)	0	(0)
+350	Nongan	0 ± 00	0.0	(0.0)	0	(0)
	Dongjin	0 ± 00	0.0	(0.0)	0	(0)
-150	Unvegetated	51 ± 39	—		—	

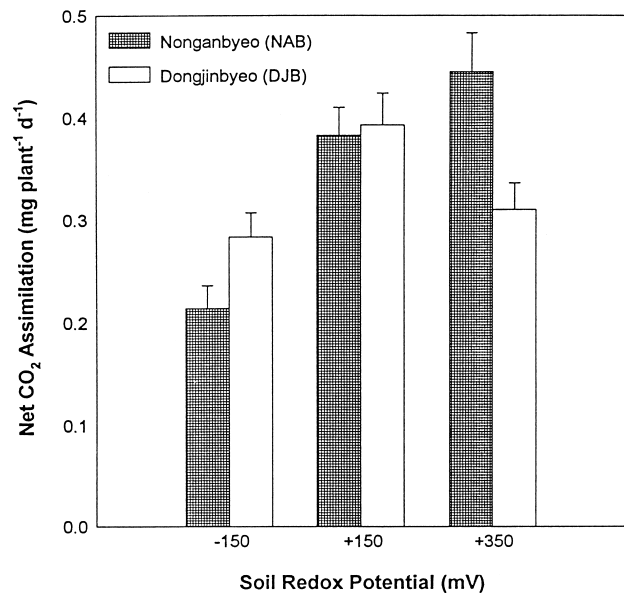
Data on methane production are means of three replications with standard deviation. Data on methane emission were obtained under light and dark conditions; data in parenthesis were obtained under dark conditions.

1993). DJB had both a lower root weight and a higher CH₄ production than NAB (Tables 1 and 2). Methane emission through plant was enhanced by soil methane production at -150 mV. The amount of methane emitted by DJB was slightly higher than that of NAB. Methane emission may be cultivar-specific. Even though DJB emitted only 2.0~2.4% of soil methane produced, the amount was 50 times higher than that produced through NAB. The lower percentage of CH₄ emitted indicates that DJB either has limited gas transport capacity or higher CH₄ oxidation in or around the roots. To discover the mechanism responsible additional research is needed. Wang et al. (1997) reported a statistically significant high correlation between methane emission rates and root dry weight.

The rate of CH₄ emission from rice plant under light and dark conditions is also shown in Table 2. The rate of CH₄ emission was lower under dark than under light conditions. A possible explanation could be differences in stomatal opening and transpiration rate. Gas exchange in the plants occurs through a vascular system, which is the most important organ for transpiration (Pezeshki and DeLaune, 1996; Conrad, 1940). The vascular system serves as a channel for the supply of O₂ from the top to the base of the plant and for the transpiration of water and gases from roots to leaves (Armstrong, 1979).

Net Photosynthesis

Net carbon dioxide assimilation (NCA) of the two rice varieties was also affected by soil Eh (Figure 1). There was less photosynthetic activity for both varieties at -150 mV compared to +150 mV and +350 mV. Under strongly reduced soil conditions (-150 mV) net CO₂ assimilation was reduced for both varieties. The reduction in net CO₂ assimilation in NAB was greater than in DJB at -150 mV. Under moderately reduced conditions (+150 mV and +350 mV) net CO₂ assimilation was greater as compared to plants grown at -150 mV. These results suggested that reduced and moderately reduced soil conditions (+150 mV and +350 mV) enhanced net CO₂ assimilation of both rice varieties.

**Figure 1.** Net carbon assimilation of rice plants under different redox potentials in laboratory conditions.

Radial Oxygen Loss

Figure 2 shows the rate of radial oxygen loss (ROL) from the two rice varieties growing under different soil redox potentials. ROL was Eh-dependent, with more O₂ leaking from the rice roots at highly reduced conditions (-150 mV) than under moderately reduced soil conditions (Figure 2). Armstrong (1979) reported that the effectiveness of gas transport depended on two factors: (1) physical resistance to diffusion and, (2) O₂ demand along the diffusion path. There were no significant differences in ROL between the varieties at the Eh studied. Differences in ROL do not seem to be significant for NAB at - or +150 mV. Given the high CH₄ production in DJB at -150 mV, the oxygen demand could be a lot higher than at +150 mV compared to NAB, but this was not true in this experiment (Figure 2). This discrepancy needs further study.

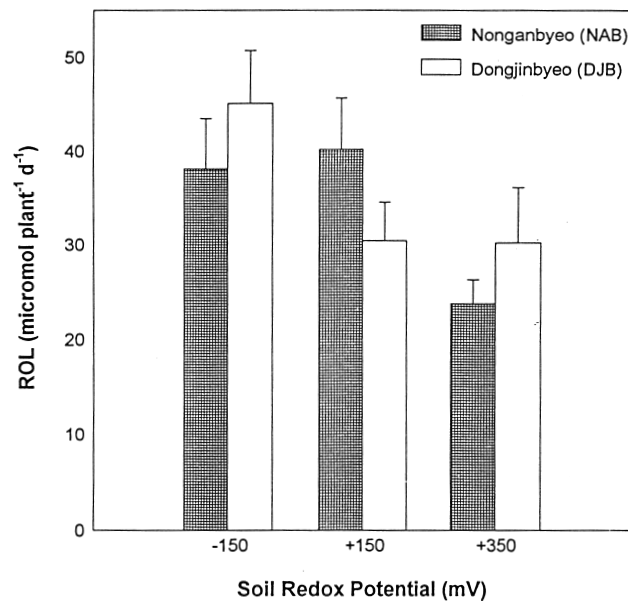


Figure 2. Radial oxygen loss (ROL) from rice roots as a function of soil redox potential.

Aerenchyma Formation

Figure 3 showed that there was a significant decrease at -150 mV between varieties in aerenchyma formation under the soil redox potentials studied. At -150 mV, DJB had a significantly greater percentage of root porosity than NAB. However, there was no significant difference at +150 mV and +350 mV. This result showed that the development of root aerenchyma in the rice plants studied was not impacted by moderately reduced soil conditions (+150 mV and +350 mV). Kludze et al. (1994) reported that aerenchyma formation in rice could be a genetic trait that expresses itself spontaneously. Thus, additional studies are needed to evaluate the response of aerenchyma formation in rice cultivars at various reduced soil conditions. Kludze et al. (1993) reported that root porosity shows a trend similar to ROL. However, this relationship was not found in this study. The significant effects of the redox potential conditions on root aerenchyma development and on the high values of root porosity (>50%) in the two rice cultivars imply that this wetland crop is very well adapted to reduced and moderately reduced conditions (+150 mV and +350 mV), as compared to strongly reduced conditions (-150 mV). The reduction in the root porosity of the two varieties at -150 mV can be attributed to the more strongly reduced conditions.

In conclusion the results of this study demonstrated that rice plant adaptation and physiological function are governed by soil redox condition. Root length and weight decreased in plant growth under strongly reduced conditions (-150 mV). The amount of CH₄ production and emission was dependent on redox condition. Methane production was observed only at -150 mV. Net carbon assimilation in rice was influenced by soil redox condition. Greatest CO₂ fixation was observed at moderately reduced

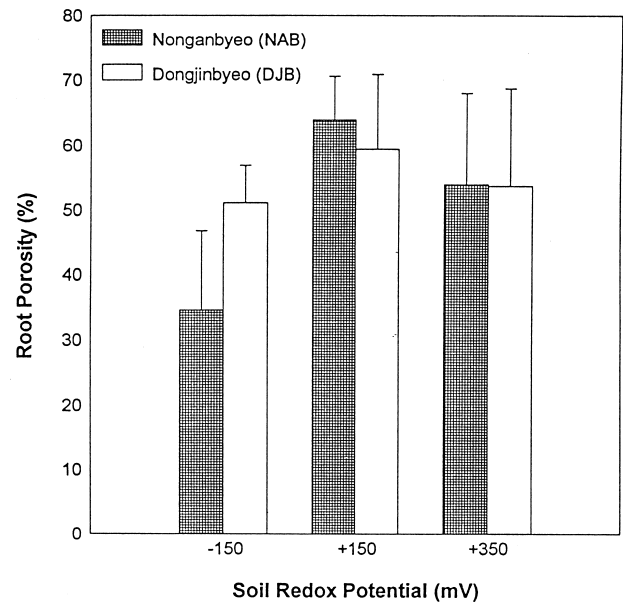


Figure 3. Root aerenchyma (as root porosity) development in rice as a function of soil redox potential.

conditions (+150 mV and +350 mV). Radial oxygen loss was generally increased with intensity of soil reduction.

There was a remarkable difference between cultivars. One variety (NAB) had reduced growth under low redox while the other variety (DJB) showed no significant effects. The cultivar (DJB) which was less effected by low redox had high CH₄ production in soil but emitted only a small percent to the atmosphere. The high CH₄ produced by DJB and low percentage emitted may be due to its physiological adaptation to growing under low soil redox conditions. These results have important implications for mitigating methane emission and breeding or developing rice cultivars. Field trials of these cultivars under a range of soil redox conditions is needed to confirm this laboratory data. Additional research on root exudation by these cultivars in relation to CH₄ production and emission and on the ability to maintain plant production under reduced soil conditions is also needed.

Acknowledgements. This study was supported in part by National Research Council, IAEA Fellowship Program, 2101 Constitution Avenue, TJ21151, Washington, D.C. 20418-0007. The authors wish to express their gratitude to Dr. C.W. Lindau for his assistance in the gas chromatograph operation.

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在控制的氧化還原狀況下生長之韓國水稻品種 其生理功能及甲烷和氧之交換

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本研究將兩種韓國水稻植株 (Nonganbyeo 和 Dongjinbyeo) 在室內條件下培養於土壤懸液中，觀測植株生長，通氣組織形成，徑向氧釋放，淨二氧化碳同化作用和甲烷的產生與釋放。土壤為美國 Crowley 水稻土，並控制在不同氧化還原狀況下 (-150, +150 和 +350 mV)。與中度還原狀況相比，Nonganbyeo 的株高、根長、乾重和碳固定量在強還原條件下 (-150 mV) 一般都降低，而 Dongjinbyeo 只觀測到二氧化碳固定量的降低。強還原條件下 (-150 mV)，植株根孔隙度低於培養在其他兩個較高氧化還原狀況下 (+150 和 +350 mV) 的植株。由於甲烷產生在強還原條件下 (-150 mV)，所以中度還原條件下培養的水稻植株沒有甲烷的釋放。然而，甲烷產生的強還原條件下，兩種水稻植株的甲烷釋放不同。淨二氧化碳同化作用依土壤 Eh 而不同。兩植株的淨光合速率在還原狀況下 (Eh -150 mV) 降低，而徑向氧釋放量在 Eh -150 mV 最大，這可能是由於還原土壤中氧的需要量較大。結果表明，土壤還原程度可影響水稻植株的生長和甲烷的釋放。管理實踐中，應考慮使水稻生長在中度還原條件下，以使碳的固定處於最佳。這種條件下生長還可減少甲烷向大氣的排放。

關鍵詞：通氣組織形成；二氧化碳固定；韓國；甲烷釋放；*Oryza sativa*；徑向氧釋放。