

Phyton (Horn, Austria)	Vol. 40	Fasc. 1	43–55	30. 6. 2000
------------------------	---------	---------	-------	-------------

Scanning Electron Microscopy Analysis of the Aerenchyma in Two Rice Cultivars

By

Klaus BUTTERBACH-BAHL*), Hans PAPEN*) and Heinz RENNENBERG*)

With 3 Figures

Received May 20, 1999

Accepted July 27, 1999

Key words: *Oryza sativa* L., cultivar Lido and Roma, aerenchyma, scanning electron microscopy, CH₄-concentration within the shoot-aerenchyma.

Summary

BUTTERBACH K., PAPEN H. & RENNENBERG H. 2000. Scanning electron microscopy analysis of the aerenchyma in two rice cultivars. – *Phyton* (Horn, Austria) 40 (1): 43–55, with 3 figures. – English with German summary.

The anatomy and construction of the aerenchyma of two different rice cultivars that differed in gas transport capacity through the aerenchyma was studied by scanning electron microscopy in different parts of the rice plants (root, root-shoot transition, leaf sheath, leaf blade, and stem), with special emphasis to limitations of gas transport within the plant and gas exchange between the aerenchyma and the soil or the aerenchyma and the atmosphere. Differences in the construction or aerial extend of the aerenchyma between the two cultivars were not observed. Measurements of CH₄-concentrations within the aerenchyma of the leaf sheaths and the internodes of the stem, as well as of the aerial extend of the aerenchyma indicate that CH₄ is released from rice aerenchyma to the atmosphere mainly via the leaf sheet. Apparently, the parenchymous cell layer that separates root and shoot aerenchyma provides the major resistance to gas transport within the rice plant. Further studies are required to identify features of this cell layer that mediate differences in gas transport resistance.

Zusammenfassung

BUTTERBACH K., PAPEN H. & RENNENBERG H. 2000. Rasterelektronenmikroskopische Untersuchungen am Aerenchym von zwei Reissorten. – *Phyton* (Horn, Austria) 40 (1): 43–55, 3 Abbildungen. – Englisch mit deutscher Zusammenfassung.

*) K. BUTTERBACH-BAHL, H. PAPEN, H. RENNENBERG, Fraunhofer Institut für Atmosphärische Umweltforschung, Kreuzeckbahnstr. 19, D-82467 Garmisch-Partenkirchen, Germany.

An zwei Reisvarietäten, die in vorangegangenen Freiland- und Labor-Untersuchungen Unterschiede in der Gastransportkapazität des Aerenchymsystems zeigten, wurden rasterelektronenmikroskopische Untersuchungen zur Beschreibung der Anatomie und Konstruktion des Aerenchymsystems in verschiedenen Pflanzenabschnitten (Wurzel, Wurzel-Sproß-Übergang, Blattscheide, Blattspreite, Halm) durchgeführt. Die Untersuchungen konzentrierten sich auf die Identifizierung a) von Restriktionen des Gastransports innerhalb des pflanzlichen Aerenchmys sowie b) morphologischer Voraussetzungen für den schon früher beobachteten Gasaustausch zwischen Boden und Aerenchym bzw. Boden und Atmosphäre. Es konnten keine signifikanten Unterschiede in der räumlichen Ausdehnung bzw. der Anatomie des Aerenchmys zwischen den beiden untersuchten Reisvarietäten nachgewiesen werden. CH_4 -Konzentrationsmessungen in verschiedenen Sproßabschnitten zeigten, daß die Emission von CH_4 aus dem pflanzlichen Aerenchym in die Atmosphäre im wesentlichen über die Blattscheiden erfolgte. Als hauptsächlicher Restriktor des Gastransports im pflanzlichen Aerenchymssystem erwiesen sich Lagen parenchymatischer Zellen (Dicke ca. 40–50 μm), die zwischen Wurzelaerenchym und Aerenchym des Sprosses gefunden wurden. In zukünftigen Arbeiten sollten die Eigenschaften dieses den Gasaustausch innerhalb der Pflanze modulierenden Gewebeabschnitts verstärkt untersucht werden.

1. Introduction

Like other wetland plants which are growing in waterlogged soils, rice plants develop an extensive aerenchyma in order to supply the roots with oxygen (e.g. CRAWFORD 1982, JUSTIN & ARMSTRONG 1987, NEUE & SASS 1994). Since the aerenchyma is not gas-tight with respect to the environment, gas exchange between both the soil and the aerenchyma as well as the atmosphere and the aerenchyma can be observed. Rice roots are surrounded by a 1–4 mm oxic zone, which is due to the radial oxygen loss from rice roots (ARMSTRONG 1971a). The “oxidizing” power of rice roots protects the rice plants against phytotoxic concentrations of reduced substances like Fe^{2+} and H_2S (TROLLENIER 1988, GREEN & ETHERINGTON 1977). Moreover, the loss of oxygen by rice roots into an anaerobic environment has a strong impact on the consumption of methane in paddy soils. DE BONT & al. 1978 have shown that the loss of oxygen by rice roots stimulates methanotrophic bacteria, which colonize the aerobic zone surrounding the roots, the root surface or even the aerenchyma itself (GILBERT & FRENZEL 1995, BOSSE & FRENZEL 1997). It is estimated that up to 40% of potential CH_4 emission from the soil into the atmosphere is oxidized in the rhizosphere of rice plants (EPP & CHANTON 1993, DENIER VAN DER GON & NEUE 1996). The role of the aerenchyma system of rice plants for methane emissions from rice paddy fields has been intensively studied (SEILER & al. 1984, HOLZAPFEL-PSCHORN & al. 1985, DENIER VAN DER GON & VAN BREEMEN 1992, BUTTERBACH-BAHL & al. 1997) and it has been demonstrated that plant mediated transport through the aerenchyma is the major pathway for CH_4 -emission from rice paddy fields for rice plants older than 30–40

days (SCHÜTZ & al. 1989, BUTTERBACH-BAHL & al. 1997). Results from field measurements over an entire vegetation period indicate that more than 80% of the CH_4 emitted from a rice field was emitted via plant mediated transport, whereas other emission pathways, i.e. diffusion through the water column and release of gas bubbles, are of minor importance (BUTTERBACH-BAHL & al. 1997). Apparently the rice aerenchyma is of crucial importance for the emission of the radiatively active trace gas CH_4 from paddy soils to the atmosphere (BUTTERBACH-BAHL & al. 1997). There is strong evidence that rice cultivars differ in the magnitude of CH_4 -emissions from rice paddy fields (LINDAU & al. 1995, WATANABE & al. 1995, SIGREN & al. 1997, BUTTERBACH-BAHL & al. 1997) and that these differences are at least partly due to differences in plant mediated transport between the cultivars. In a field and laboratory study BUTTERBACH-BAHL & al. 1997 showed that differences in the gas transport capacity of the aerenchyma between two Italian rice cultivars (Roma and Lido) were responsible for the significant differences in CH_4 -emissions observed in the field. The reason for the differences in gas transport capacity between the cultivars were assumed to be due to anatomical differences of the rice aerenchyma. The aim of this study was to analyse the anatomy of the aerenchyma system of the two Italian rice cultivars Lido and Roma that differ in gas transport capacity by scanning electron microscopy in order to identify differences which may explain the differences in CH_4 emission observed.

2. Materials and Methods

Anatomical studies of the aerenchyma system of rice plants were carried out with two Italian rice cultivars, *Oryza sativa* L. Var. japonica type Roma and type Lido. Seeds of both cultivars were supplied by the Istituto per la Risiicoltura (Vercelli, Italy). Plant material used in this study was derived either from rice plants cultivated under greenhouse conditions or from rice plants grown under natural conditions at fields of the Istituto per la Risiicoltura (BUTTERBACH-BAHL & al. 1997). Rice plants grown under greenhouse conditions (air temperature 20–25 °C, light intensity 350–450 $\mu\text{E m}^{-2} \text{ sec}^{-1}$, photoperiod 14 h) were cultivated in liquid culture media as described by BOUREAU 1977. The pH of the media was adjusted regularly to pH 6.0 with 1 M NaOH. Plants used for anatomical studies were at least 2 weeks old, i.e. in the vegetative stage before tillering, and at maximum 90 days old, i.e. at the beginning of the reproductive stage.

Rice aerenchyma was characterized with a scanning electron microscope (SEM). For this purpose pieces of roots, stems, and leaves were fixed in glutaraldehyde-paraformaldehyde as described by ROSENBAUER & KEGEL 1978. After several dehydration steps with increasing ethanol concentrations (20–50–70–80–90–95–99.9% ethanol) the plant material was critical-point dried with CO_2 (Balser, Liechtenstein) and then sputtered with gold (Leitz, Wetzlar, Germany) in order to increase electrical conductivity. The SEM used in this study was a Cambridge Sterio Scan S4 (Cambridge, UK). During SEM studies, probes were rotated and slightly tilted if it was necessary to improve the observation of morphological structures of the rice aer-

enchyma. Since the tilt was generally below 15° its effects on magnification was not considered. The aerial extend of the aerenchyma system of the rice plants at distinct cross-sections was measured by planimetric determination from photographs using a delta T Area Meter (Delta-T Devices, UK).

Concentrations of methane in the aerenchyma of leaf sheets and stem internodes of adult rice plants (approx. 100 days old), which had been grown in the field, were determined in August 1990 by carefully taking 100 μ l samples of aerenchyma air sample from the aerenchyma using a gas tight syringe (Hamilton, Switzerland). Air samples were directly injected into a GC system equipped with a flame ionisation detector and analysed for methane. Analytical conditions used for the determination of methane were as previously described (BUTTERBACH-BAHL & al. 1997). The data obtained were subjected to analysis of variance and multiple range tests by ANOVA (SPSS for Windows 7.0, SPSS Inc.).

3. Results

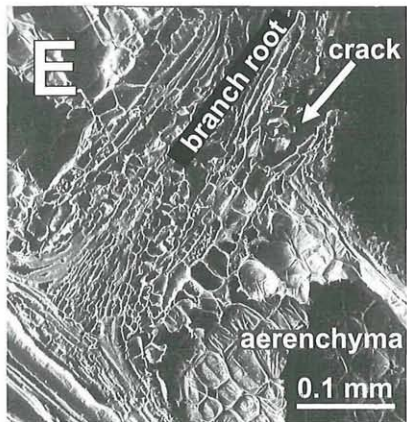
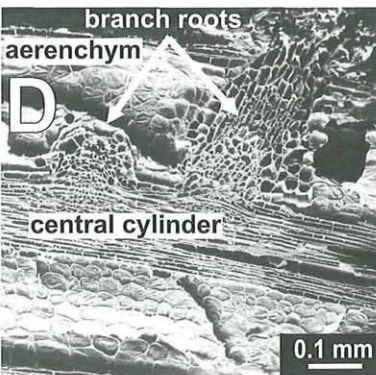
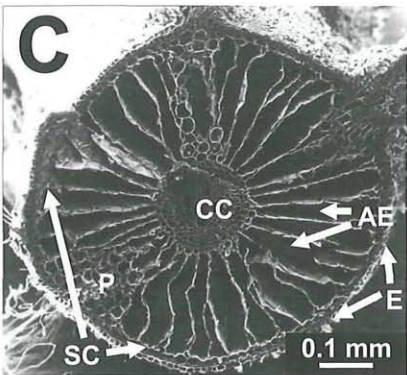
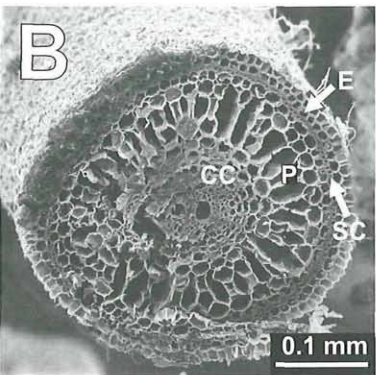
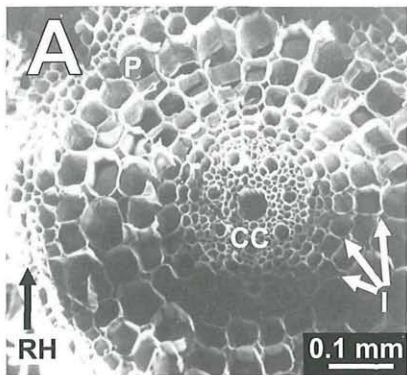
The aerenchyma of rice plants was investigated using plants in the vegetative and reproductive stage. At both stages the aerenchyma was well established. The aerial extend of the aerenchyma was investigated in different plant parts.

Root aerenchyma

The root-aerenchyma develops in successive stages during growth of the root. In the fine roots, close to the root tip, aerenchyma was not detectable (Fig. 1A). Gas exchange in this part of the root is restricted to diffusion through intercellulars. These intercellulars have an aerial extend of 1–2% of the total root-cross section.

More adult, mature parts of the roots showed 2–3 cell layers of sclerenchyma cells below the exodermal cell layer (Fig. 1B). These sclerenchyma cells become a secondary exodermis and fulfil a protective function for the root, since the exodermis dies and sloughs off as root development proceeds. The aerenchyma arises lysigeniously from degeneration of cortical cells in the basal parts of the roots. Some degenerated and collapsed cortical cells constituted long continuous or discontinuous bands,

Fig. 1. A) Root cross-section close to the root tip. Intercellulars (I), parenchymatic or cortical cells (P), the central cylinder (CC) and the rhizodermis (RH) are indicated. Cultivar Roma (13 days old); B) and C) Cross sections of an younger and older basal part of a rice root exhibiting two different stages of root aerenchyma development. In B) the degeneration of cortical cells to the aerenchyma is less pronounced than in C). Exodermis (E), sclerenchymatous cylinder (SC), parenchymatic or cortical cells (P), aerenchyma (AE) and the central cylinder with the vascular tissues (CC) are indicated. B) cultivar Lido (39 days old); C) cultivar Lido (72 days old); D) Longitudinal section of a mature root showing the aerial extend and construction of root aerenchyma as well as the development and break through of branch roots. Cultivar Lido (72 days old); E) Longitudinal cross section of a mature root showing the break through



of a branch root through the sclerenchymatous cylinder and the exodermis of the main root. The crack indicated is supposed to be the main location for the diffusional exchange of gases between the atmospheres of the soil and the aerenchyma. Cultivar Lido (72 days old).

which separate the aerenchyma into different compartments. The centre of the root contains the vascular tissues. A cross section of the root resembles on a wheel with spokes (Figs. 1B, C). The relative contribution of the root aerenchyma to the total root-cross section was $52.4 \pm 10.2\%$ ($n = 16$) for rice plants of the type Lido and $45.4 \pm 4.8\%$ for the type Roma ($n = 5$), respectively. The values were not significantly different at the number of roots analyzed. Figure 1D shows a longitudinal section of an older root, demonstrating the huge extend of the root aerenchyma and its three dimensional arrangement. Emerging branch roots can partly interrupt these regular continuous aerenchyma system and, therefore, may limit gas exchange within the root. Moreover, branch roots may play an important role for the gas exchange with the soil atmosphere, since at the location where the branch root breaks through the exodermis of the main root, a deep crack was always visible, which seems to be directly connected to the root aerenchyma (Fig. 1E). Therefore, the sites where branch roots emerge from the main roots may be considered significant for the diffusional exchange of gases between the soil- and the aerenchyma-atmosphere.

Aerenchyma in the root-shoot transition

The roots and the leaf sheets were inserted at the root-shoot transition. The root-shoot-transition therefore must represent that part of the plant, where the aerenchyma of the leaves joins the aerenchyma of the roots (Fig. 2A). For all rice plants investigated ($n > 35$) a direct connection of the root aerenchyma system with the leaf sheet aerenchyma could not be demonstrated. Both aerenchyma systems, though adjacent, were always separated by a parenchymatous cell layer with a thickness of approximately 40–50 μm . Thus, gas exchange between the root aerenchyma and the leaf aerenchyma is restricted within the root-shoot transition zone to intercellulars.

Aerenchyma in the leaf sheath

The leaf sheath envelops the basal parts of the shoot, thereby protecting the young shoot and the bud. The aerenchyma system of the leaf sheath consists of 8–9 large pronounced and 4–5 smaller less pronounced lacunae. The relative contribution of the aerenchyma system to the total area at a distinct leaf sheath cross section was up to 70% (Fig. 2B). The diameter of the larger lacunae is approximately 90–400 μm for younger plants, and approximately 0.2 cm for rice plants of an age of more than 80 days, respectively. The large lacunae are regularly intercepted horizontally (0.2–0.3 cm for younger plants and 0.5–1.0 cm for older plants) by stellate cells as shown in Figure 2C. Abundant pores with diameters of 2–15 μm are visible in this stellar cell layer so that the sectional appearance of the leaf blade lacunae may not have any influence on the diffusional flow of gases

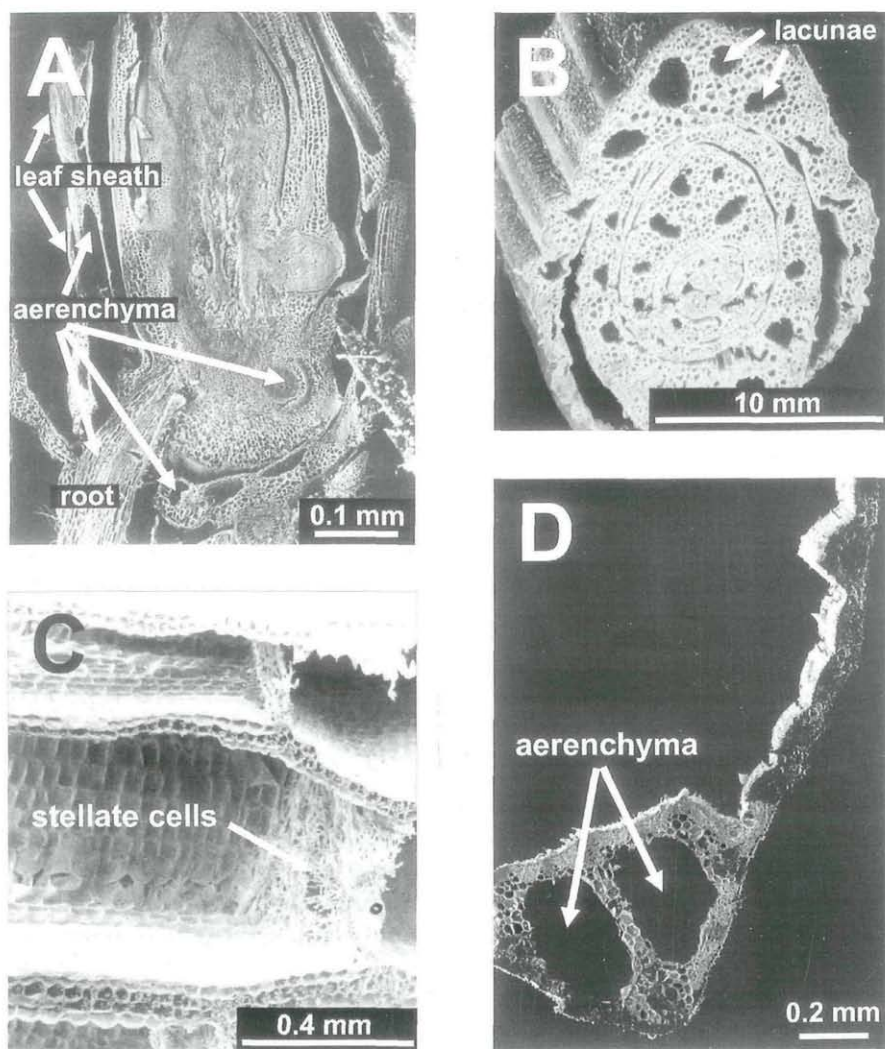


Fig. 2. A) Longitudinal section of the root-shoot-transition of a 17 days old rice plant. Inserting roots, as well as the aerenchyma systems of the root and the leaf sheath were indicated. Cultivar Roma (17 days old). B) Cross section of a young shoot, demonstrating the huge aerial extend of the aerenchyma of the leaf sheath. Cultivar Roma (39 days old); C) Longitudinal section of a leaf sheath showing the interception of leaf sheath lacunae by stellate cells. Cultivar Lido (72 days old); D) Cross section of a leaf blade. The two aerenchyma channels are indicated. Cultivar Lido (72 days old).

through the aerenchyma. Intercellulars between the epithel cells which form the walls of the lacunae can only be found at the sites where the vascular bundles are present. These intercellulars are closely related to the stomata, which are also situated close to the vascular bundles. Nevertheless, a direct link of lacunae and stomata could not be demonstrated. Micropores, which have been described by NOUCHI & al. 1990 as a direct link between the lacunae of the leaf sheet and the atmosphere have not been found in the cultivars investigated.

Aerenchyma in the leaf blade

The aerenchyma of the leaf blade was restricted mostly to two lacunae which are positioned to the left and the right of the central vascular bundle. The diameter of the lacunae is 0.03–0.04 cm for older leaves and, thus, an order of magnitude smaller than the lacunae of the leaf blade (Fig. 2D). Numerous stomata were found at both sites of the leaves (120–180 stomata mm^{-2}). The stomata are found on the leaf blade surface in longitudinal rows. The opening width of the stomata was for all rice plants investigated 1 μm irrespective whether leaf sheaths or leaf blades were studied. A direct link between the stomata and the aerenchyma lacunae was not found. Thus, a link of the stomata with the lacunae via intercellulars must be assumed.

Aerenchyma of the stem

The internodes of mature stems were hollow ($\varnothing$ 1–2 mm) and additional aerenchyma channels with diameters of 0.1–0.2 mm embedded by parenchymatous cells were found between vascular bundles of the stem walls (Fig. 3). In contrast to the vast aerenchyma system of the internodes, no aerenchyma was detectable within the nodes. At the nodes a parenchymatic barrier (diaphragm) of approximately 0.3 mm thickness separate the large internodal lacunae of the stem. The aerenchyma channels found in the walls of the internodes were interrupted within the nodes. The basal internodal lacunae were not directly connected with the root aerenchyma in the root-shoot transition zone, as also found out for the aerenchyma of the leaf sheaths. Compared to the leaf sheaths, enveloping the stem, the extend of the aerenchyma of the stem was much smaller and, thus, is unlikely to be significantly involved in the internal gas exchange within the rice plant.

CH_4 -concentrations of the aerenchyma of leaf sheaths and stem internodes

Measured CH_4 -concentrations in the leaf sheaths and internodes decreased with increasing sampling height along the rice plant. The basal leaf blade, which inserts the shoot below the floodwater level, showed the highest CH_4 -concentrations within the aerenchyma (1610 ± 1900 ppmv),

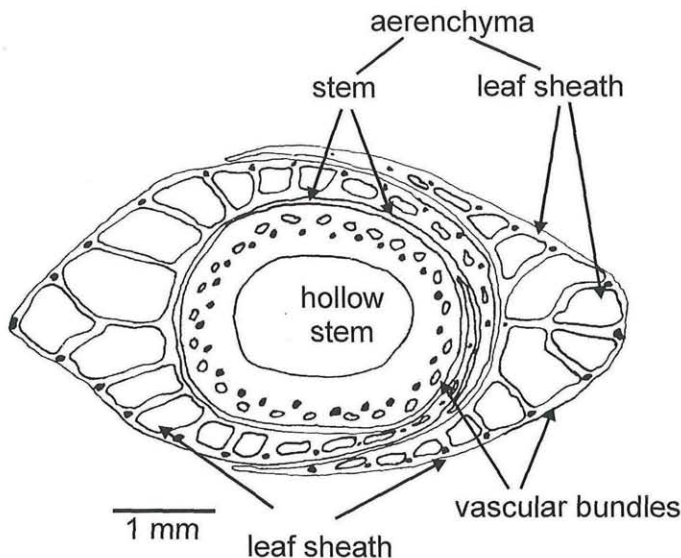


Fig. 3. Schematic drawing of an internode cross-section, showing the distribution and location of aerenchyma in a culm internode.

whereas the 4th leaf blade, which inserts the shoot above the floodwater level, showed methane concentrations in the aerenchyma of 9.2 ± 7.8 ppmv (Table 1). CH_4 -concentrations in the large lacunae of the stem internodes were generally higher than CH_4 -concentrations of the leaf blade aerenchyma. Highest CH_4 -concentrations of 5990 ± 3950 ppmv were observed in the lacunae of the most basal internode. The 4th internode, at a sample height of 44–60 cm showed CH_4 -concentrations of 620 ± 470 ppmv (Table 1).

Table 1.

CH_4 concentrations ($\pm$ SE) in the aerenchyma of leaf sheets and internodes of adult rice plants (Cultivar Roma). Indices a to c indicate significant differences at 95% confidence level.

	Sampling height above floodwater level [cm]	CH_4 -concentration [ppmv]	N
1. leaf sheet	5–12	1610 ± 775^a	6
2. leaf sheet	12–27	210 ± 58^b	5
3. leaf sheet	25–43	56 ± 38^c	5
4. leaf sheet	35–50	9.2 ± 3.4^c	5
1. Internode	2–6	5990 ± 1317^a	9
2. Internode	12–15	4250 ± 595^a	5
3. Internode	28–46	1865 ± 272^b	7
4. Internode	44–60	620 ± 192^c	6

Differences between the aerenchyma of both cultivars studied

Though the aerenchyma of both rice cultivars have been studied intensively, and investigations focused on differences between the cultivars, no significant differences have been found in the anatomy of the aerenchyma. The extend of the aerenchyma in different plant parts as well as the width of intercellulars or stomata were comparable for both cultivars investigated.

4. Discussion

The general construction of the rice aerenchyma is of fundamental importance for the understanding of gas exchange between the soil and the atmosphere and for the plant mediated CH_4 -emissions from rice paddy fields. From the data obtained it is supposed that CH_4 -uptake from the soil into the aerenchyma of the rice root mainly occurs where branch roots break through the exodermis of the main root. This hypothesis is further supported by observations of ARMSTRONG 1971a and FLESSA & FISCHER 1992 who demonstrated that increased O_2 -losses to the sediment, i.e. gas exchange between the aerenchyma and the soil is favoured in these root sections. A break down of the root aerenchyma system at the root sections, from which branch roots emerge, as described by ARMSTRONG 1971b, was not observed in this study. The aerenchyma of the root of the rice cultivars studied was continuous up to the root-shoot transition zone.

The root-shoot transition zone seems to have a crucial importance for the exchange of gases between the rhizosphere and the atmosphere, since this part of the plant seems to act as a barrier for gas transport. Indirect evidence that the root-shoot-transition zone is the rate limiting structure of rice plants for gas exchange within the rice aerenchyma was provided by DENIER VAN DER GON & VAN BREEMEN 1993. Tracer gas experiments by BUTTERBACH-BAHL & al. 1997 have unequivocally confirmed this hypothesis. The morphological studies presented here further support the significance of the root-shoot transition zone for the gas exchange in rice aerenchyma, since the aerenchyma of the root did not join directly the aerenchyma of the leaf sheath or the culm, as supposed by ARASHI & NITTA 1955. Thus, gas exchange must be restricted to intercellulars in this part of the rice plant. Apparently, the parenchymous cell layer that separates root and shoot aerenchyma provides the major resistance to gas transport within the rice plant. Further studies are required in order to identify features of this cell layer that mediates differences in gas transport resistance.

Since CH_4 is emitted by plant mediated transport from the soil to the atmosphere high concentrations of CH_4 can be found in medullar cavities of the leaf sheath and the internodes of the stem (WANG & al. 1997). Based

on CH₄-concentration measurements in the leaf sheath lacunae and stem internodes it can be hypothesized that the emission of CH₄ from the rice aerenchyma to the atmosphere occurs mainly from the leaf sheaths. In these measurements a rapid decrease of CH₄-concentrations was found within the lacunae-system of the leaf sheaths with increasing plant height, which was more pronounced than the decrease of CH₄-concentrations within stem internodes. This hypothesis is supported by the present anatomical studies. The leaf sheaths exhibited a vast aerenchyma system and envelop the shoot during the early stages of rice plant development. These findings are consistent with results by NOUCHI & al. 1990, who also described that the main site of CH₄-release is the leaf sheath. Still also the nodes may be an important site of CH₄ release from the rice aerenchyma to the atmosphere. This was pointed out by WANG & al. 1997 who injected air in the medullar cavities and observed that air bubbles were not only released rapidly from the leaf sheaths but also from the junction points of nodes.

NOUCHI & al. 1990 described micropores in the basal parts of the leaf sheath for the Japanese rice cultivar Koshohikari. These micropores were smaller and anatomically different from stomata and were considered the main site for plant mediated CH₄-emissions. This observation was not confirmed for the Italian rice cultivars Lido and Roma investigated in this study. Thus, it must be concluded that the stomata of the leaf sheaths were the main site of CH₄-release to the atmosphere for the rice cultivars analyzed in this study. Using scanning microscopy it was not possible to demonstrate differences in anatomy of the aerenchyma between the two cultivars studied, though differences in gas transport capacity were found between the aerenchyma system of these rice cultivars (BUTTERBACH-BAHL & al. 1997). Comparable results were also obtained by ARMSTRONG 1969, who described significant differences in rhizosphere oxidation capacity of different rice cultivars, but was unable to attribute these observations to differences in anatomy of the aerenchyma. It must be concluded that anatomical differences, which lead to differences in gas transport through the aerenchyma, cannot be detected by SEM, since the three dimensional structure of the aerenchyma cannot be totally resolved by this technique. More sophisticated techniques, e.g. the use of computer-tomography may be useful to identify differences in the aerenchyma of rice plants exhibiting different methane transport capacities from soil into the atmosphere.

5. Acknowledgements

The authors would like to thank Dr. U. RICHTER (Botanical Institute of the Justus Liebig University, Giessen, Germany) for valuable discussions and support in scanning electron microscopy.

6. References

- ARASHI K. & NITTA H. 1955. Studies on the lysigenous intercellular space as the ventilating system in the culm of rice and some other graminaceous plants. – Proceedings of the Crop Science Society of Japan 24: 78–81.
- ARMSTRONG W. 1969. Rhizosphere oxidation in rice: an analysis of intervarietal differences in oxygen flux from the roots. – *Physiologia Plantarum* 22: 296–303.
- 1971a. Radial oxygen losses from intact rice roots as affected by distance from the apex, respiration and waterlogging. – *Physiologia Plantarum* 25: 192–197.
- 1971b. Oxygen diffusion from the roots of rice grown under non-waterlogged conditions. – *Physiologia Plantarum* 24: 242–247.
- BOSSE U. & FRENZEL P. 1997. Activity and distribution of methane-oxidizing bacteria in flooded rice soil microcosms and in rice plants (*Oryza sativa*). – *Appl. Environ. Microbiol.* 63: 1199–1207.
- BOUREAU M. 1977. Application de la chromatographie en phase gazeuse à l'étude de l'exsudation racinaire du riz. – *Cahiers Orstom, sér. Biol.* 12, 2: 75–81.
- BUTTERBACH-BAHL K., PAPEN H. & RENNENBERG H. 1997. Impact of gas transport through rice cultivars on methane emission from rice paddy fields. – *Plant, Cell and Environment* 20: 1175–1183.
- CRAWFORD R. M. M. 1982. Physiological responses to flooding. – In: LANGE O. L., NOBEL P. S., OSMOND C. B. & ZIEGLER H. (Eds.), *Physiological plant ecology II*, pp. 454–477. – Springer-Verlag, Berlin.
- DE BONT J. A. M., LEE K. K. & BOULDIN D. F. 1978. Bacterial oxidation of methane in a rice paddy. – *Ecological Bulletin* 26: 91–96.
- DENIER VAN DER GON H. A. C. & VAN BREEMEN N. 1993. Diffusion-controlled transport of methane from soil to atmosphere as mediated by rice plants. – *Bio-geochemistry* 21: 177–190.
- & NEUE H. U. 1996. Oxidation of methane in the rhizosphere of rice plants. – *Biol. Fertil. Soils* 22: 359–366.
- EPP M. A. & CHANTON J. P. 1993. Rhizospheric methane oxidation determined via methyl fluoride inhibition technique. – *J. Geophys. Res.* 98: 18413–18422.
- FLESSA H. & FISCHER W. R. 1992. Plant induced changes in the redox potentials of rice rhizospheres. – *Plant and Soil* 143: 55–60.
- GILBERT B. & FRENZEL P. 1995. Methanotrophic bacteria in the rhizosphere of rice microcosms and their effect on porewater methane concentration and methane emission. – *Biology and Fertility of Soils* 20: 93–100.
- GREEN M. S. & ETHERINGTON J. R. 1977. Oxidation of ferrous ion by rice (*Oryza sativa* L.) roots: a mechanism for waterlogging tolerance? – *Journal of Experimental Botany* 28: 678–690.
- HOLZAPFEL-PSCHORN A., CONRAD R. & SEILER W. 1985. Production, oxidation and emission of methane in rice paddies. – *FEMS Microbiology Ecology* 31: 343–351.
- JUSTIN S. H. F. W. & ARMSTRONG W. 1987. The anatomical characteristics of roots and plant response to soil flooding. – *New Phytologist* 106: 465–495.
- LINDAU C. W., BOLLIH P. K. & DELAUNE R. D. 1995. Effect of rice variety on methane emission from Louisiana rice. – *Agricul. Ecosyst. Environ.* 54: 109–114.

- NEUE H. U. & SASS R. L. 1994. Trace gas exchange in rice cultivation. – In: PRINN R. G. (Ed.), *Global atmospheric-biospheric chemistry*, pp. 119–147. – Plenum Press, New York, London.
- NOUCHI I., MARIKO S. & AOKI K. 1990. Mechanism of methane transport from the rhizosphere to the atmosphere through rice plants. – *Plant Physiol.* 94: 59–66.
- ROSENBAUER K. A. & KEGEL B. H. 1978. *Rasterelektronenmikroskopische Technik*. – Thieme Verlag, Stuttgart, New York.
- SCHÜTZ H., SEILER W. & CONRAD R. 1989. Processes involved in formation and emission of methane in rice paddies. – *Biogeochemistry* 7: 33–53.
- SEILER W., HOLZAPFEL-PSCHORN A., CONRAD R. & SCHARFFE D. 1984. Methane emissions from rice paddies. – *J. Atmos. Chemistry* 1: 241–268.
- SIGREN L. K., BYRD G. T., FISHER F. M. & SASS R. L. 1997. Comparison of soil acetate concentrations and methane production, transport, and emission in two rice cultivars. – *Global Biochem. Cycles* 11, 1–14.
- TROLLENIER G. 1988. Visualisation of oxidizing power of rice roots and of possible participation of bacteria in iron deposition. – *Zeitschrift für Pflanzenernährung und Bodenkunde* 151: 117–121.
- WANG B., NEUE H. U. & SAMONTE H. P. 1997. Role of rice in mediating methane emission. – *Plant and Soil* 189: 107–115.
- WATANABE A., KAJIWARA M., TASHIRO T. & KIMURA M. 1995. Influence of rice cultivar on methane emission from paddy fields. – *Plant and Soil* 176: 51–56.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Phyton, Annales Rei Botanicae, Horn](#)

Jahr/Year: 2000

Band/Volume: [40_1](#)

Autor(en)/Author(s): Buttenbach-Bahl Klaus, Papen Hans, Rennenberg Heinz

Artikel/Article: [Scanning Electron Microscopy Analysis of the Aerenchym in Two Rice Cultivars. 43-55](#)