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Relationship between wet tolerance, anatomical structure of aerenchyma and gas exchange ability among several plant species

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Summary

Eight plant species were grown both under normal and high soil moisture conditions, and the wet tolerance among plant species was analyzed in relation to the tolerance to low oxygen concentration, high Mn concentration, and combined tolerance in water culture experimnts. Under the current experimental conditions, although the wet tolerance was positively correlated with the combined tolerance to low oxygen and high Mn concentrations, tolerance to low oxygen concentration was a more influential factor. The most significant characteristics of the mineral status of the plant tops grown under high soil moisture conditions were the low K content and the high Mn content. The tolerance to low oxygen concentration of the excised roots did not correspond either to the tolerance to low oxygen concentration or the wet tolerance of intact plants.

Wet sensitive plant species hardly develop an aerenchyma throughout the plant, whereas wet tolerant plant species except for adzuki bean develop a lysigenous aerenchyma throughout the plant in proportion to the degree of wet tolerance. Adzuki bean was comparatively tolerant to a high soil moisture level through the development of adventitious roots from the base of the stem.

Effective gas exchange between the atmosphere and the soil atmosphere in waterlogged soil could be mediated by the presence of a well-developed lysigenous aerenchyma throughout the whole plant. Reed showed a marked development of the lysigenous aerenchyma, resuting low methane and high nitrogen gas concentrations in waterlogged soil. One gram of reed shoot was estimated to be able to decrease or increase approximately 1 vol % of methane or nitrogen gas concentration in the soil atmosphere.

These results suggest that the lysigenous aerenchyma throughout the whole plant may contribute to the wet tolerance and effective gas exchange between the atmosphere and the soil atmosphere under high soil moisture conditions, espcially under waterlogged soil conditions.

Key Words：barnyardgrass, gas exchange, lysigenous aerenchyma, methane, nitrogen gas, reed, rice, upland crops, wet tolerance

Introduction

Various kinds of gases are exchanged between plants and the atmosphere or soil atmosphere (HIGUCHI 1978 : LEE et al. 1981 ; MINAMI 1982 ; STÜNZI and KENDE 1989 ; YOSHIDA and BROADBENT 1975 ; YOSHIDA et al. 1975) . This gas exchange is of particular interest in media high moisture or anaerobic conditions.

High tolerance of rice to submerged soil is ascribed to the capacity of oxygen supply to the roots from the shoots (AIMI 1960) , or high activity of glycolic acid oxidase in the roots (MITSUI et al. 1964 ; MITSUI and KUMAZAWA 1961 ; MITSUI et al. 1961) .

Numerous investigations on the lysigenous intercellular spaces which act as a ventilating system in plants, i. e., rice, upland crops or several weeds, have been carried out in relation to wet tolerance (ARASHI and NITTA 1955 ; ARIKADO 1954, 1955, 1959a, 1959b ; ARIKADO and ADACHI 1955) .

Waterlogging damage in wheat was attributed to the decrease of the concentration of dissolved oxygen in the soil solution (TROUGHT and DREW 1980) . However, a relatively high concentration of O_2 was observed in wheat roots after the excision of shoots (ERDMANN and WIEDENROTH 1988) . In the yellow waterlily, gases within the plant flow between the rhizome and the atmosphere through pressurized ventilation (DACEY 1980, 1981 ; DACEY and KLUG) .

The emission of methane in the atmosphere has been increasingly implicated in the greenhouse effect and the destruction of the ozone layer, and methane emission from plants or individual ecosystems has been estimated (CICERONE et al. 1983 ; DACEY and KLUG 1979 ; HOLZAPFEL-PSCHORN et al. 1986 ; HOLZAPFEL-PSCHORN and SEILER 1986 ; MINAMI and YAGI 1988 ; SEILER et al. 1984 ; SHEPPARD et al. 1982) .

The objectives of the present investigation are (1) to analyze the mechanism of wet tolerance associated with the development of lysigenous intercellular spaces in the roots, culm and lef sheaths, (2) to study the anatomical structure of several plant species, and (3) to estimate the degree of gas permeability within a plant especially methane and nitrogen gases in several plant species.

Materials and Methods

Soil culture experiment

Soil was collected from fields in the farm of Yamagata University (Fluvisols) where in the previous year, Chinese cabbage [*Brassica campestris* . L. (pekinensis group)] had been cultivated and harvested. The soil was air-dried, passed through a 5-mm mesh sieve, and mixed with $(NH_4)_2SO_4$, KCl and $NaH_2PO_4 \cdot 2H_2O$ (reagent grade) at the rate of 5 g each of N, P_2O_5 and K_2O per 30 kg air-dry soil. Thirty kg of this air-dry soil was packed in a polypropylene container 22 cm deep×67 cm long×40 cm wide. Deionized water was added to the fertilized soil in order to maintain field water conditions for 15 days. Seeds of two barnyardgrass cultivars (*Echinochloa crus-galli* Beauv., *Echinochloa oryzicola* Vasing) and Japanese radish [*Raphanus sativus* L. (daikon group) cv. Minowase No. 3] were sown 15 days prior to the two soil moisture treatments ; seeds of adzuki bean (*Vigna angularis* cv. Takara) and wheat (*Triticum aestivum* L. cv. Hanagasa) were sown 10 days before the treaments ; however, rice (*Oryza sativa* L. cv. Sasanishiki) , reed [*Phragmites australis* (Cav.) Trin. ex Steudel] and head lettuce [*Lactuca sativa* L. (capitata group) cv. Great lake] were transplanted as 16-, 30- and 38-day-old seedlings, respectively. In the duplicated polypropylene containers, each plant species was planted in one row with different orders. Two soil moisture treatments, namely, normal and high moisture, were prepared ; the former was approximately equivalent to the field moisture, and the latter approximately equivalent to the maximum water capacity. Appropriate amounts of deionized water were supplied continuously for 16 days along with the decrease of the soil moisture. Consequently, the soil moisture content was 18 and 44% of water on a dry soil weight basis, respectively. The pH and Eh of the respective soils were measured periodically.

Each subsample consisted of 1 to 8 plant tops ; four replicates were harvested. The other experimental procedures were decribed elsewhere (WAGATSUMA et al. 1989).

Water culture cxperiment

Seeds of the first plant group, i. e., two barnyardgrass cultivars, reed, rice and head lettuce, as well as the second plant group, i. e., wheat, and the third plant group, i. e., adzuki bean and Japanese radish, were sown 6, 3 and 2 weeks prior to the treatments, respectively. After germination, these seedlings were grown in half strength of the standard nutrient solution until the treatments were applied.

Four treatment solutions were prepared : normal oxygen and normal Mn concentrations (A) , normal oxygen and high Mn concentrations (AM) ; low oxygen and normal Mn concentrations (N) ; oxygen and high Mn concentrations (NM) . The solution with a low oxygen concentration was prepared by bubbling nitrogen gas continuously into the nutrient solution. The flow rate of nitrogen gas was regulated by measuring the concentration of dissolved oxygen in the treatment solution several times a day. The solution with a normal oxygen concentration was prepared by bubbling air into the medium. The average concentration of dissolved oxygen in the normal and low oxygen treatments was 7 and 1 ppm O_2, respectively. Normal and high Mn concentrations were set at 1 and 50 ppm, respectively. The pH of the medium was maintained at 5.2. The treatments were continued for 17 days. Four replicated samples were harvested. Other conditions were described elsewhere (WAGATSUMA 1989).

Experiment on tolerance to low oxygen concentration

Six plant species, i. e., rice, reed, adzuki bean, head lettuce, wheat and Japanese radish, were grown normally for one month in a standard nutrient solution. Experiment on the tolerance of intact plants was carried out as follows : Four polypropylene containers were filled with tap water, adjusted to pH 5.0, and maintained at 30℃. Two treatments were prepared, i. e., normal and low oxygen treatments. The former was prepared by bubbling air, and the latter by bubbling nitrogen gas. When the concentration of dissolved oxygen in the medium decreased to less than 1 ppm, all the plants (8 plants per species) were transferred into the medium. The concentration of dissolved oxygen was maintaied in the range from 0.3 to 1.5 ppm and the plants were harvested 1, 5, 10 and 24 hr after the initiation of the treatments. Ca, Mg, K and P contents of the roots were determined.

Experiment on the tolerance of excised roots was carried out as follows : White fibrous roots were sampled from 5 to 10 normally grown plants per species and cut into 2 to 3 cm segments. Well-mixed excised roots were divided into 10 portions, and each portion was transferred into a polyethylene bag perforated with the needle of a sewing machine. Five liter of tap water adjusted to pH 5.0 was poured into the polypropylene containers, bubbled with nitrogen gas, and maintained at 30℃. After the concentration of dissolved oxygen decreased from 0 to 0.5 ppm, the respective two polyethylene bags were sampled at, 1, 5, 10 and 24 hr after the initiation of the treatments.

Anatomical study on the aerenchyma in plant

The plant samples cultured normal conditions were used for the investigations on the anatomical structure of the aerechyma by scanning electron microscopy, light microscopy or stereoscopic microscopy.

For scanning electron microscopy, reed, rice and wheat plants were grown in water culture, and the two *Echinochloa* sp. in waterlogged soil. Other experimental procedures were the same as those previously described (WAGATSUMA 1989).

For light or stereoscopic microscopy, reed, rice, adzuki bean, head lettuce, wheat and Japanese radish plants were grown in water culture. Sections cut by hand with a razor blade were stained with a 0.01% methylene blue solution for 3 to 5 min and washed with deionized water.

Air permeability within reed plant

Air permeability within the plants was measured under negative pressure ; one culm was inserted into a glass column (1.5 cm of inside diameter and 100 cm long) filled with water, and the volume of the evolved ges was measured. The inserted culm had been cut at various heights from the surface of waterlogged soil in the pot.

Gas emission from reed plant

Concentrations of gases, namely, oxygen, nitrogen gas and methane, were analyzed using a gas chromatographic technique (Hitachi 163 Gas chromatograph, 3 mm×2.0 m steel column packed with 80～100 mesh Molecular Sieve

5A). The soil atmosphere was periodically collected from the water-logged soil in the pots in which reed had been transplanted at various densities. Other details were described elsewhere (WAGATSUMA 1989).

Results and Discussion

Plant growth and specific symptoms observed in soil culture and water culture

Under high soil moisture conditions, the plants from the two *Echinochloa* sp. as well as the reed, and rice plants grew better than under normal conditions; adzuki bean plants also grew well with faint leaf color, and they developed a large amount of adventitious roots near the soil surface; the growth of head lettuce was slightly abnormal, and the lower leaves senesced early; wheat growth was retarded, and the lower leaves senesced early; Japanese radish plants showed immediately severe chlorosis, wilted leaves, the growth was considerably retarded, and part of the plants withered up. No symptoms of Mn toxicity were observed.

In water culture, Mn toxicity symptoms developed under treatment with high Mn concentration, but no

Table 2. Wet tolerance and tolerance to other treatments

Plant species	W.T.	N/A	AM/A	NM/N	NM/A
E. crus-galli Beauv.	268	68	105	99	67
Reed	253	67	91	145	98
E. oryzicola Vasing	255	85	97	115	97
Rice	215	90	64	74	67
Adzuki bean	183	87	43	54	47
Head lettuce	87	74	60	89	65
Wheat	58	64	48	78	50
Japanese radish	10	44	85	83	37

W.T.=wet tolerance, N/A=tolerance to low oxygen concentration, AM/A=Mn tolerance at normal oxygen concentration, NM/N=Mn tolerance at low oxygen concentration, NM/A=combined tolerance to high Mn and low oxygen concentrations.

Table 3. Mean values of mineral contents of tops of 8 plants grown in different media

		P %	K %	Ca %	Mg %	Fe ppm	Mn ppm	Na %
Water culture	A	0.549	3.76	0.663	0.457	119	168	0.267
	N	0.517	2.71	0.457	0.440	89	146	0.213
	NM	0.520	2.91	0.446	0.358	56	1828	0.237
Soil culture	Normal moisture	0.476	5.15	1.10	0.482	127	350	0.184
	High moisture	0.506	4.10	1.37	0.506	146	490	0.334

symptoms of low oxygen concentration were observed.

Wet tolerance was in the following order; two *Echinochloa* sp., reed>rice, adzuki bean≫head lettuce >wheat>Japanese radish (Table 2). Tolerance to low oxygen concentration (N/A) was high in rice, adzuki bean and *E. oryzicola*, and low in Japanese radish. Mn tolerance (AM/A) was high in the two *Echinochloa* sp. and reed, and low in adzuki bean and wheat. Combined tolerance to high Mn and low oxygen concentrations (NM/A) was high in reed and *E. oryzicola*, and low in wheat, adzuki bean and Japanese radish.

Mean values of mineral contents of the tops of the 8 plants grown in the different media are shown in Table 3. In water culture, the K and Ca contents were obviously lower at low oxygen concentrations; under the combined conditions, the contents of K, Ca, Mg and Fe were lower, but that of Mn was considerably higher. In soil culture, the K content was lower, and Mn content was higher under high soil moisture conditions.

In fresh soils after cultivation, no signficant differences were detected in the content of water soluble nitrate ion and exchangeable bases, especially K (Table 1). The lower K content of the tops under high soil moisture conditions was therefore ascribed to the low oxygen concentration.

Under high soil moisture conditions, the K content of the plant tops was higher than that under normal conditions, while the Ca, Mg and Mn contents were lower

Table 1. Chemical properties of fresh soils after cultivation

Parameters (on dry soil basis)	Normal soil moisture conditions	High soil moisture conditions
Average pH (H_2O)	5.26	5.69
Average Eh (mV)	375	235
Total C (%)	1.74	1.75
Total N (%)	0.33	0.29
Water soluble NO_3-N*1 ($mg \cdot 100 g^{-1}$)	0.88	0.65
Exchangeable bases ($meq \cdot 100 g^{-1}$)		
Ca	8.4	9.6
Mg	5.2	6.2
Na	0.40	0.34
Exchangeable Mn (ppm)*2	22	20
Available P*3 ($mg\ P_2O_5 \cdot 100 g^{-1}$)	1.7	1.4

*1 : measured with ion electrode
*2 : extracted with N ammonium acetate (pH 7.0)
*3 : Truog-P

Table 4. Correlation coefficients between wet tolerance and mineral content ratio of the tops of plants grown under two moisture conditions

P	K	Ca	Mg	Fe	Mn	Na
0.490	0.936**	−0.794*	−0.912**	−0.664	−0.759*	0.210

** significant at 1 % level, * significant at 5 % level.

(Table 4).

The relationship between the mineral content of the plant tops grown in soil culture and in water is shown in Table 5. At high Mn and normal oxygen concentrations, no correlation was observed under high soil moisture conditions. At low oxygen concentrations, the K content ratio of the plant tops was positively correlated with that under high soil moisture conditions. At high Mn and low oxygen concentrations, the P, K and Fe content ratios were positively, and Mg content ratio negatively correlated with those under high soil moisture conditions, respectively.

As no differences were observed between the two soils in the amount of exchangeable Ca, Mg and K or available P (Table 1), the data suggest the following: (1) under high soil moisture conditions, K absorption may be inhibited by the low oxygen concentration in the medium, (2) under high soil moisture conditions, the absorption of Ca and Mg may be increased by the inhibition of the absorption K, and (3) Mn toxicity may also be associated in part with the growth retardation under high soil moisture conditions, though the experimental soil was not a Mn toxic one (when dry soil was used for the measurement, the amount of exchangeable Mn and 0.5% tannic acid reducible Mn was equivalent to 3.7 and 7.0 ppm on a dry soil basis (WAGATSUMA 1989).

Since the average values of the redox potential of soils with normal and high moisture levels were 375 and 235 mV, respectively (Table 1), it is assumed that divalent Mn ion may be formed and denitrification may be initiaed (MARSCHNER 1986).

Although the nitrogen content of the plant tops was not determined in the present investigation, nitrogen deficiency may not be the cause of the poor growth under

Table 5. Correlation coefficients between the correspondent mineral content ratio of the tops of plants grown in soil culture and in water cultures §

	P	K	Ca	Mg	Fe	Mn
AM/A	0.261	−0.164	−0.461	−0.672	0.361	0.623
N/A	0.411	0.926**	−0.259	−0.587	0.075	−0.552
NM/A	0.860**	0.699(*)	−0.187	−0.784*	0.972**	0.183

§ Under soil culture conditions, the mineral content ratio was calculated as the ratio of the mineral content of the plant top under normal moisture conditions to that under high moisture conditions.

** significant at 1 % level, * significant at 5 % level, (*) nearly significant at 5 % level.

Table 6. Effect of low oxygen concentration on the content ratios of Ca and K contents in the excised roots of several plant species differing wet tolerance

	Reed	Rice	Adzuki bean	Head lettuce	Wheat	Japanese radish
Ratio of Ca content*	109	170	270	200	189	185
Ratio of K content*	61	86	5	21	11	25

* ratios of Ca or K contents of the excised roots after exposure for 10 hr to low oxygen concentration to initial Ca or K contents of the excised roots.

high moisture levels judging from the small difference in the nitrate concentration between two soils (Table 1).

Tolerance to low oxygen concentration of intact plant vs excised roots

The following data were reported elsewhere (WAGATSUMA 1989) : (1) low oxygen concentration decreased considerably the K content content of excised roots in all the plant species, (2) decrease in K content was pronounced after exposure for 10 hr to low oxygen concentration, especially in adzuki bean and wheat, (3) Ca content of excised roots, on the contrary, increased following a 10 hr exposure to low oxygen concentration, especially in Japanese radish, adzuki bean and head lettuce, and (4) virtually no evident decrease in K content or increase in Ca content was observed in whole roots of intact plants even 24 hr after exposure to low oxygen concentration.

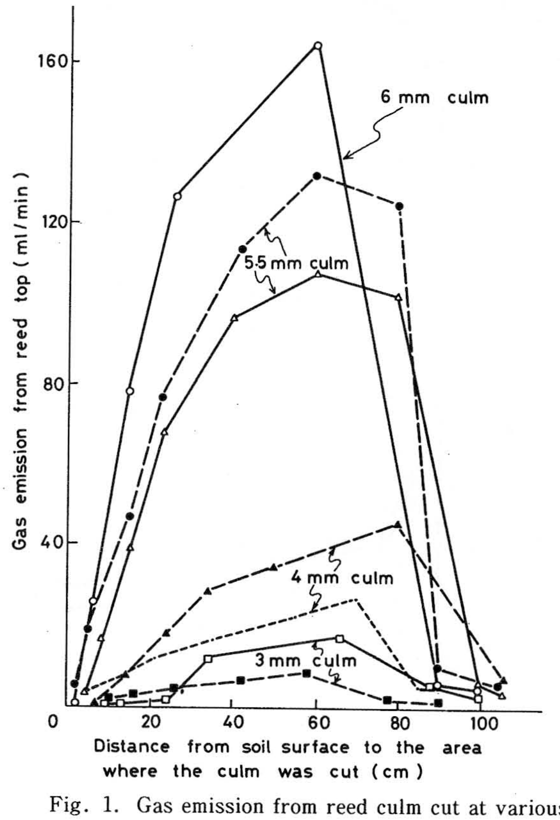


Fig. 1. Gas emission from reed culm cut at various heights from the soil surface.
*Gas emission was measured by covering the culm with a water-filled glass column 19 mm in diameter × 90 cm long. The last data on the right of each line correspond to the volume of gas emitted from intact culm. The 3 mm ~ 6 mm refers to the diameter of the basal stem.

The ratios of Ca or K contents of excised roots after exposure for 10 hr to low oxygen concentration to the initial Ca or K contents of the excised roots are shown in Table 6. The decrease in K content or increase in Ca content was not correlated with either the tolerance to low oxygen concentration or to the wet tolerance of intact plants. These data suggest that another mechanism to avoid the stress associated with low oxygen concentration may operate in the wet tolerant whole plant.

Air permeability within reed plant

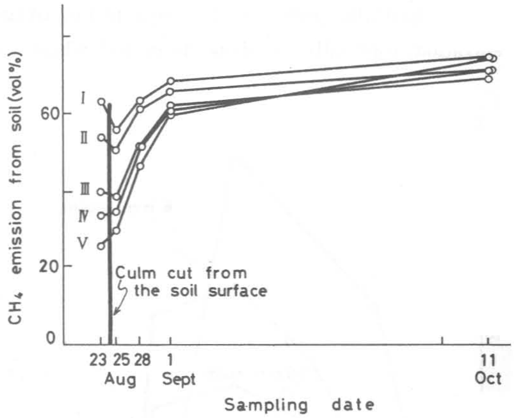
When one culm was covered with a water-filled glass column 19 mm in diameter × 90 mm long, gas was emitted from the reed culm. Gas emission was considerably enhanced when the culm was cut. The thicker the basal stem, the larger the amount of gas emitted (Fig. 1). Regardless of the size of the culm, maximum gas emission was generally observed at two thirds of the culm height from the soil surface, and the intact culm emitted approximately 5 ml/min gas. The culm position for the maximum gas emission may be controlled by the combined effect of a high negative perssure and marked development of the aerenchyma.

Anatomical structure of the plant species

Anatomical structure of the experimental plants is illustrated in Figs. 2~5. In Japanese radish, no aerenchyma was observed in the petiole (Fig. 2-a1) and thickened roots (Fig. 2-a2), whereas roots intercellular spaces were observed in the cortex (Fig. 2-a3). In wheat, no aerenchyma was observed in the midrib of the leaf (Fig. 2-b1), which the aerenchyma was partly developed at both sides of the vascular bundles and in the stomata (Fig. 2-b2) ; the aerenchyma was moderately developed in the leaf sheath (Fig. 2-b3) ; lysigenous aerenchyma was developed both in the proximal portions (Fig. 2-b4) and the middle (Fig.2-b5) of the root cortex, but in the tip portion of roots intercellular spaces were hardly observed (Fig. 2-b6). In adzuki bean, although no aerenchyma was observed both in the petiole (Fig. 3-a1) and the stem (Fig. 3-a2), the adventitious roots at base of the stem were markedly developed. In head lettuce, lysigenous aerenchyma was observed in the tip portions (Fig. 3-b1) and the middle (Fig. 3-b2) of leaf, while the root cortex showed a large amount of intercellular spaces (Fig. 3-b3). In *E. crus-galli*, a special structure was developed in the leaf sheath, i.e., a spongy network structure between the cell lines containing vascular bundles (Fig. 3-c1) ; a well-developed lysigenous aerenchyma was observed in the roots (Fig. 3-c2). In rice leaves, the intercellular spaces were well developed, especially in the midrib (Fig. 4-a1) ; lysigenous aerenchyma was considerably developed both in the proximal and middle (Fig. 4-a4) portions of the root cortex. In reed, there was a well-developed aerenchyma among the mesophyll cells of leaves (Fig. 4-b1) ; lysigenous aerenchyma present in the leaf sheath (Fig. 4-b2) , and a loose structure was observed in the center of the culm (Fig. 4-b3) ; a well-developed lysigenous aerenchyma was present in the cortex of the subterranean stem (Fig. 4-b4) ; the lysigenous aerenchyma in the cortex of roots originating from the subterranean stem was connected with the lysigenous aerenchyma in the cortex of the subterranean stem (Fig. 5-b5) ; the lysigenous aerenchyma was well-developed both in the proximal (Fig. 5-b6) and in the middle (Fig. 5-b7) portions of the root cortex, and abundant intercellular spaces were observed even in the tip portion of the roots (Fig. 5-b8).

The anatomical structures associated with wet tolerance can be summarized as follows : Japanese radish exhibits the lowest wet tolerance because the top has no aerenchyma and the roots have no intercellular spaces ; wheat and head lettuce show a comparatively high wet tolerance due to the marked development of a lysigenous aerencyma both in the top and the roots ; comparative tolerance to wet conditions of adzuki bean is ascribed to the development of adventitions roots at the base of the stem ; rice, *Echinochloa* sp. and reed exhibit a high wet tolerance because a continuous lysigenous aerenchyma is markedly developed throughout the whole plant, especially in reed.

Adventitious root development and partial development of the intercerllular spaces or lysigenous aerenchyma in the corrtex or top of plants may not enable them to withstand the considerably high level of soil moisture, i. e., waterlogged soil conditions.



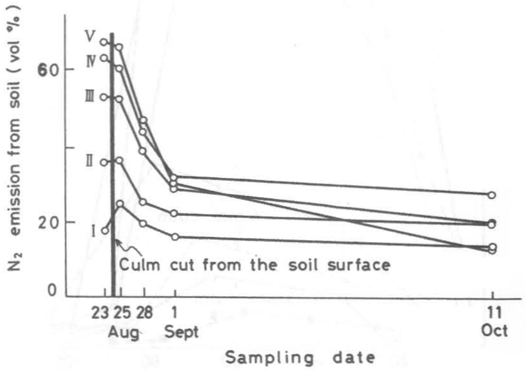


Fig. 6. Emission of methane and nitrogen gas from soil as a function of time.
* all culms in each soil pot were cut from the soil surface on 24, August. The range of dry weight of the reed tops was : I$<$10 g, 10 g$<$II$<$20 g, 20 g$<$III$<$30 g, 30 g$<$IV$<$40 g, V $>$ 40 g ; data in the figure indicate the mean value of the volume of gas emitted from soils in a few pots within each range of dry weight of the reed tops.

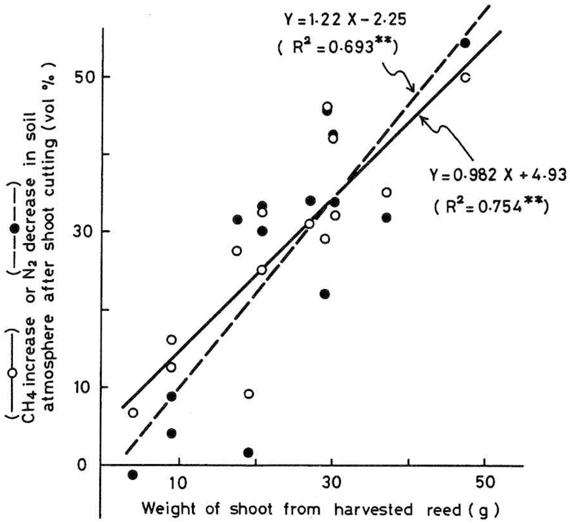


Fig. 7. Gas exchange through reed plant.

Gas exchange through reed plant

The concentration of methane or nitrogen gas in the bubbles within the waterlogged soils increased or decreased, respectively, after the culm was cut from the soil surface. The higher the culm density, the more pronounced the changes in the concentrations of methane and nitrogen gas (Fig. 6). The relationship between shoot weight of harvested reed and increase in methane or decrease in nitrogen ges concentrations in the soil atmosphere after shoot cutting is depicted in Fig. 7. Increase in methane concentration or decrease in nitrogen gas concentration was positively correlated with the shoot weight of harvested reed. Based on the regression eqations, it was estimated that one gram of reed shoot can decrease or increase approximately 1 vol % of methane or nitrogen gas in the soil atmosphere. Methane and nit-

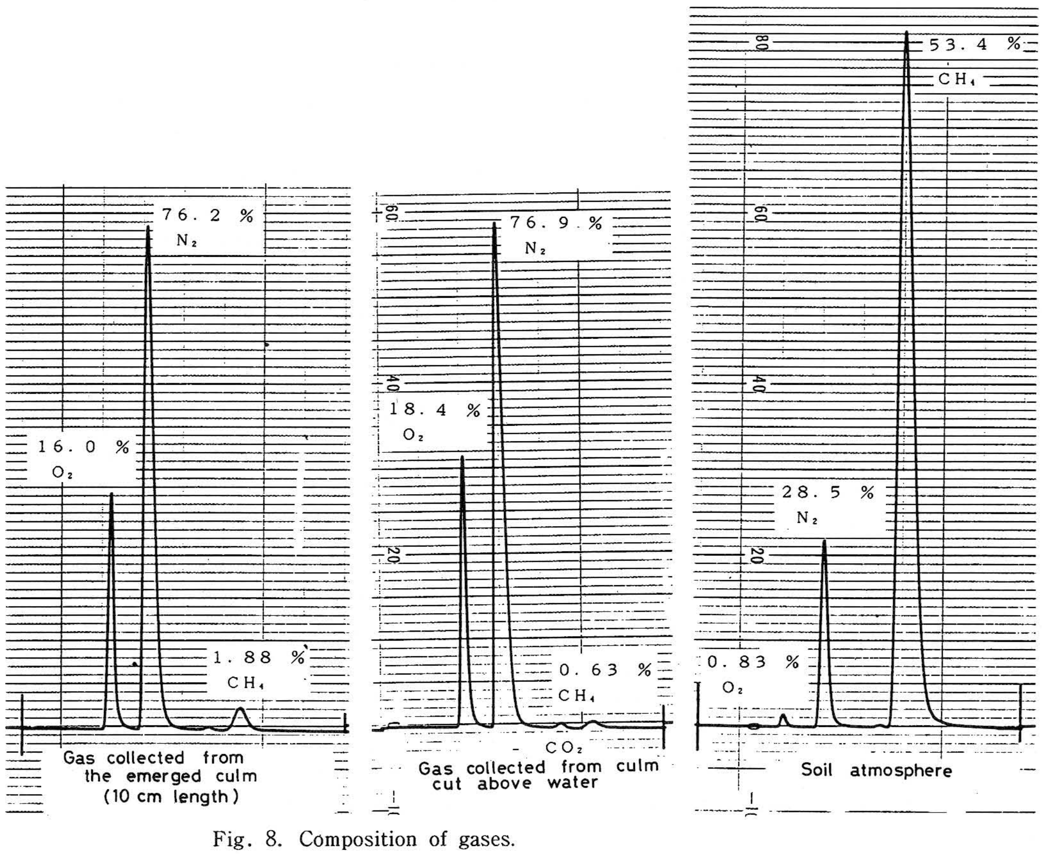


Fig. 8. Composition of gases.
* Each gas was collected from reed pots at 9 a. m. on 19, July.

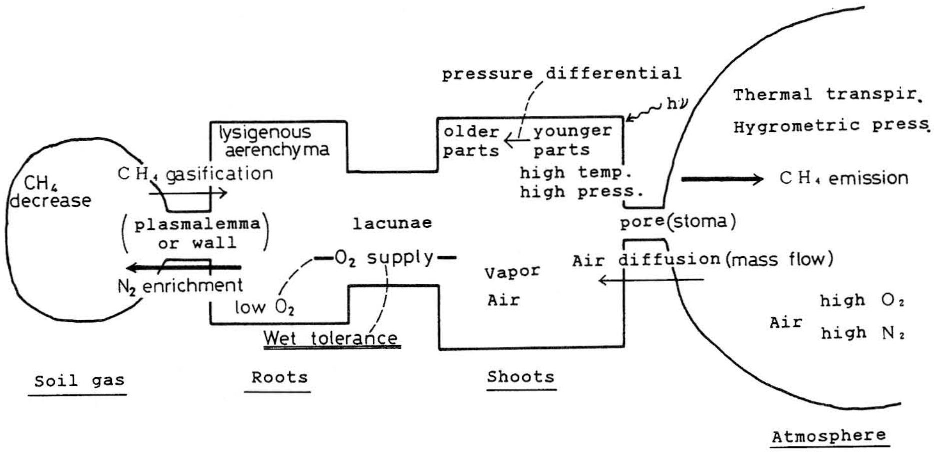


Fig. 9. Proposed mechanism of gas exchange between atmosphere and soil atmosphere.

rogen gas accounted for more than 80% of the gases. These results suggest that the reed plant may exchange gases between the amosphere and soil atmosphere. Reed plant can contribute not only to the decrease of the methane concentration in the soil atmosphere but also to the enrichment of the nitrogen concentration in the soil atmosphere. Gas exchange between atmosphere and soil atmosphere may be considerable in well-developed aerenchyma. Comparative investigations among plant species on the ability of gas exchange between atmosphere and soil atmosphere should be carried out in the future.

Reed plant can liberate a large amount of gas especially from the base of the culm into the surface water even under normal pressure in the afternoon in the summer season. The composition of the gases collected from reed plant under negative pressure is shown in Fig. 8. Although methane was actually detected, the composition of the gases was generally similar to that of the atmosphere. These results suggest the following: the tops of the reed plant may take up the gases in the atmosphere; reed roots may absorb the soil solution containing methane; methane may be gasified the root aerechyma; each gas may diffuse at different concentrations in the plant aerenchyma; methane may finally be liberated from the tops of the plant.

In conclusion, the mechanism of gas exchange between the atmosphere and the soil atmosphere proposed in Fig. 9 is mainly based on the report of Dacey (1981).

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各種植物における耐湿性，通気組織の構造および気体交換能の相互関係

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摘　　要

8種の植物を畑状態および高湿状態で栽培し，得られた耐湿性と，水耕条件での低酸素分圧耐性，耐マンガン性およびそれらの複合耐性との関連性を検討した．

本実験条件下では，耐湿性は複合耐性と有意な正の相関が成立したが，複合条件のうちでは低酸素分圧条件の方がより強い影響因子であった．高湿条件では，植物体地上部はK含有率が低下し，Mn含有率が上昇した．切断根の低酸素分圧耐性は完全植物の低酸素分圧耐性および耐湿性との対応が認められない．

耐湿性の弱い植物は体内に通気系がほとんど発達しておらず，一方アズキ以外の強い植物は耐湿性の程度に応じて体内に破生通気組織が発達していた．アズキは比較的強かったが，茎基部からの不定根の発達が顕著であった．

大気と湛水条件下の土壌空気との間のガス交換は，植物全体に連なる破生通気組織の発達によって仲介されていた．ヨシは顕著に破生通気組織が発達しており，そのために湛水条件下で土壌空気中のメタン濃度が低下し，窒素ガス濃度が上昇した．1gのヨシ地上部は土壌空気中のメタンあるいは窒素濃度を約1容積％低下あるいは上昇させる能力を有する．

以上の結果，高湿特に湛水条件では植物全体に連なる破生通気組織が耐湿性や，大気と土壌空気との間のガス交換に貢献していると示唆された．

Explanation of Figure

Fig. 2. Anatomical structure of Japanese radish and wheat.

a1 : leaf petiole of Japanese radish (×4), stereoscopic microscope after methylene blue (MB) staining.

a2 : thicked root of Japanese radish (×4), stereoscopic microscope after MB staining.

a3 : proximal portion of fibrous root of Japanese radish (×50), light microscope after MB staining.

b1 : cross- section of wheat leaf (×10), stereoscopic microscope after MB staining.

b2 : tip portion of cross- section of wheat leaf (×50), scanning electron microscope (SEM).

b3 : leaf sheath of wheat (×5), stereoscopic microscope after MB staining.

b4 : proximal portion of wheat root (×100), light microscope after MB staining.

b5 : middle portion of wheat root (×100), light microscope after MB staining.

b6 : tip portion of wheat root (×100), light microscope after MB staining.

Fig. 3. Anatomical structure of adzuki bean, head lettuce and *Echinochloa crus-galli* Beauv. (barnyardgrass).

a1 : petiole of adzuki bean leaf (×15), stereoscopic microscope after MB staining.

a2 : stem of adzuki bean (×10), stereoscopic microscope after MB staining.

b1 : middle portion of cross section of head lettuce leaf (×5), stereoscopic microscope after MB staining

b2 : proximal portion of cross section of head lettuce leaf (×5), stereoscopic microscope after MB staining.

b3 : proximal portion of head lettuce root (×50), light microscope after MB staining.

c1 : cross section of leaf sheath of *E. crus-galli* Beauv. (×200), scanning electron microscope.

c2 : root of *E. crus-galli* Beauv. (×70), SEM (artificially crushed in part).

Fig. 4. Anatomical structure of rice and reed.

a1 : cross senction of rice leaf (×10), stereoscopic microscope after MB staining.

a2 : leaf sheath of rice (×50), light microscope after MB staining.

a3 : proximal portion of rice root (×50), light microscope after MB staining.

a4 : middle portion of rice root (×100), light microscope after MB staining.

b1 : middle portion of reed leaf (×500), SEM.

b2 : middle portion of reed culm (×10), stereoscopic microscope after MB staining.

b3 : central portion of b2 (×50).

b4 : middle portion of subterranean stem of reed (×12.5), stereoscopic microscpe after MB staining.

Fig. 5. Anatomical structure (continued) and gas evolution from reed culm.

b5 : reed root originating from subterranean stem (15), stereroscopic microscope after MB staining.

b6 : proximal portion of reed root (×10), light microscope after MB staining.

b7 : middle portion of reed root (×100), light microscope after MB staining.

b8 : tip portion of reed root (×100), light microscope after MB staining.

c1 : gas evolution from young culm.

c2 : gas evolution from leaf sheath of reed culm.

Fig. 2.

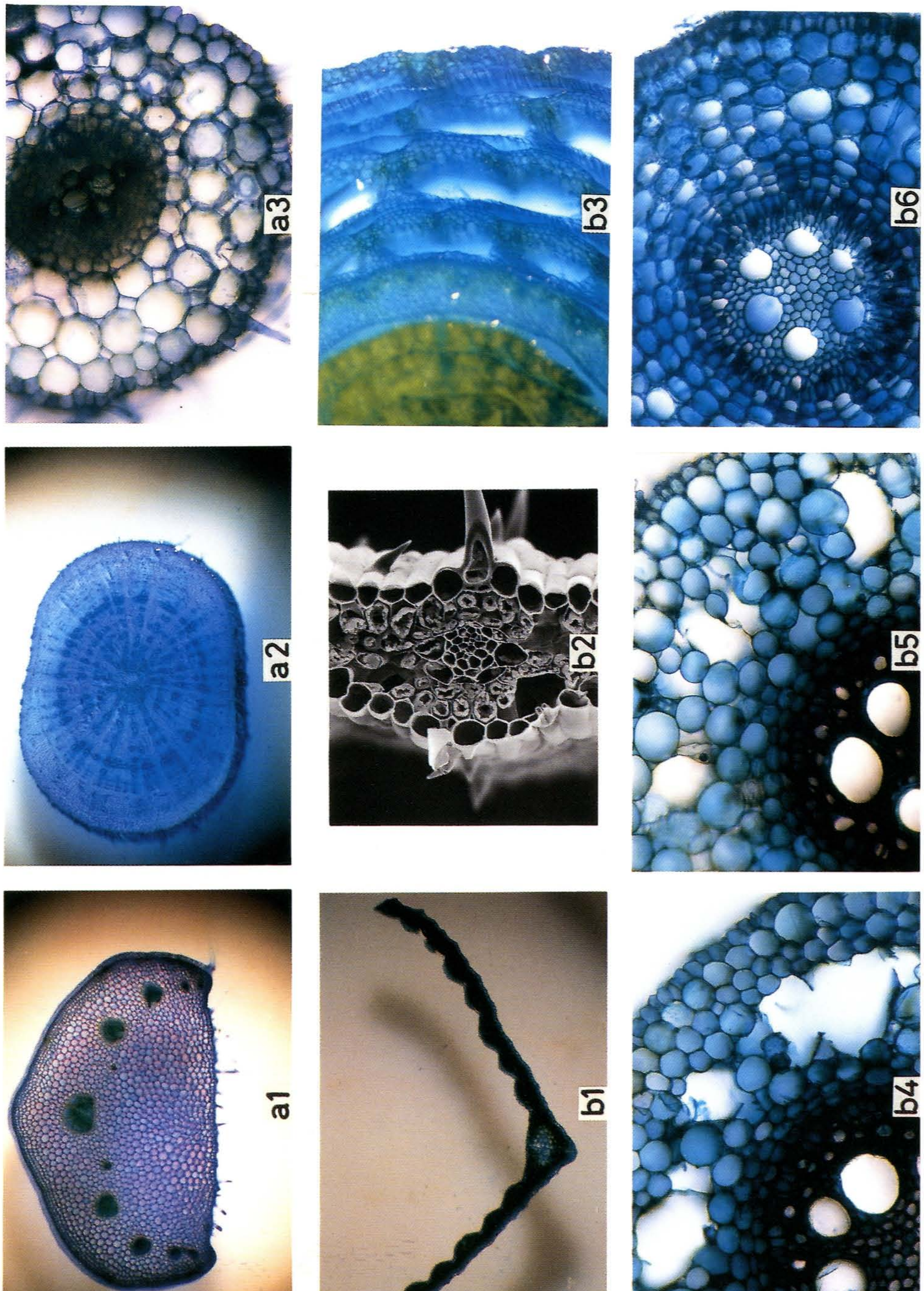

Fig. 3.

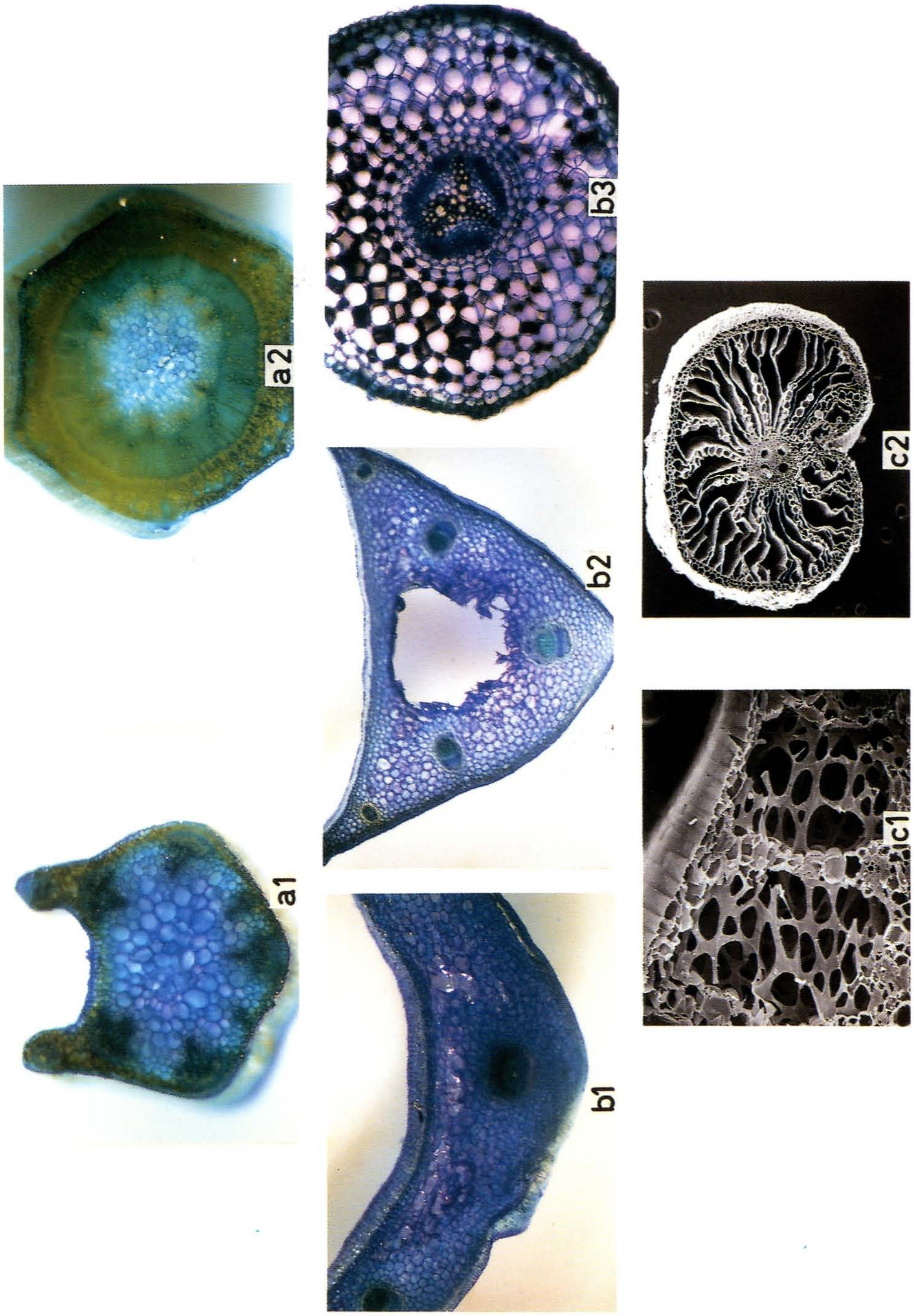

Fig. 4.

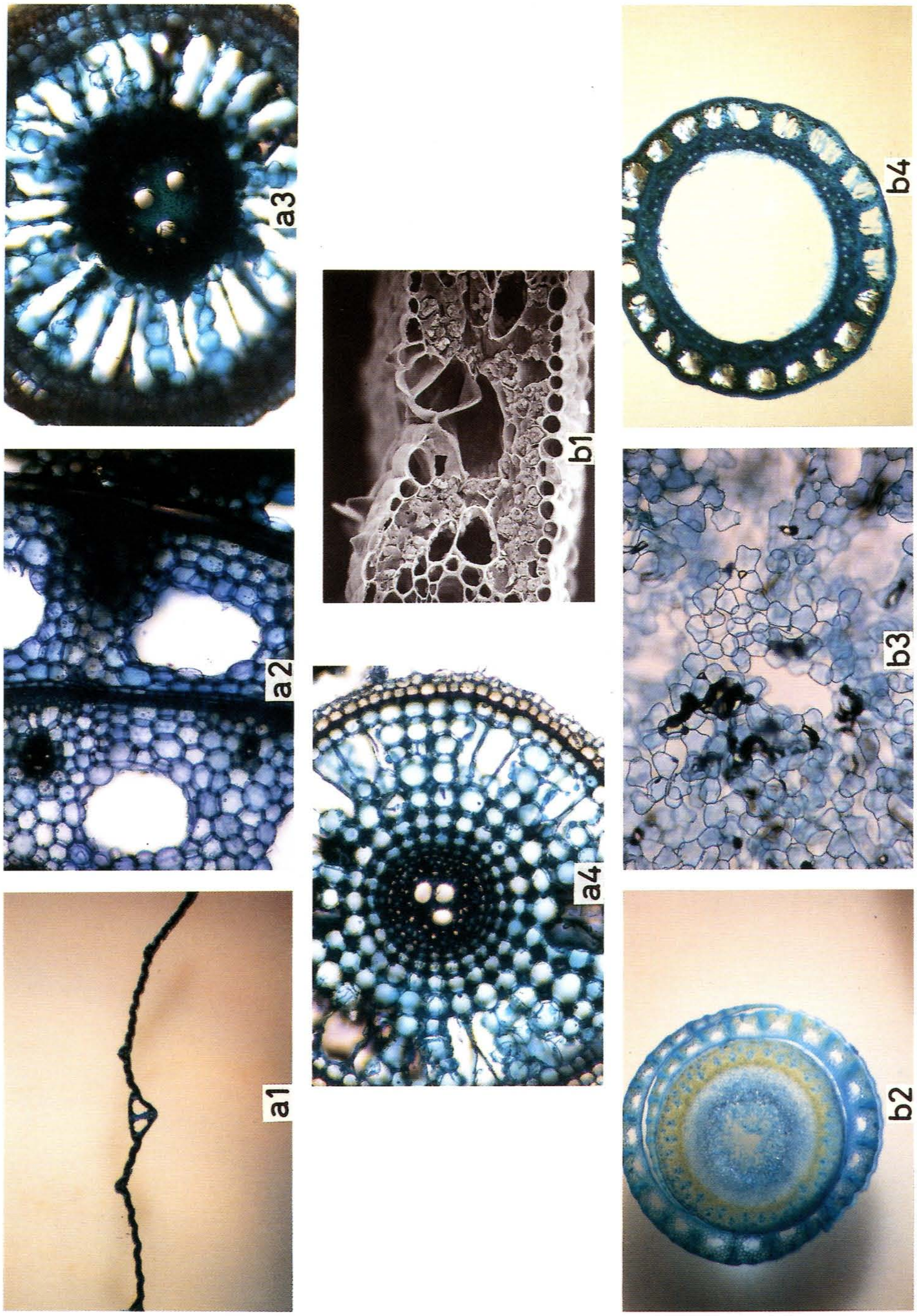

Fig. 5.