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BIOLOGICAL SULPHATE-REDUCTION IN THE SPERMOSPHERE AND THE RHIZOSPHERE OF RICE IN SOME ACID SULPHATE SOILS OF SENEGAL

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by

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Sulphate-reduction by anaerobic bacteria (Desulfovibrio and Desulfotomaculum sp.) is a process frequently described in highly reduced horizons of waterlogged soils. VAMOS (1959) BOULAINE (1960) TAKAI and KAMURA (1966) CONNEL and PATRICK (19[illegible]) BLOOMFIELD (1969).
The number of sulphate reducing bacteria increases and they produce free hydrogen sulphide when three conditions exist simultaneously : 1) anaerobiosis 2) presence of sufficient sulphates 3) presence of suitable substrates. When iron is present it immobilize free hydrogen sulphide and iron monosulphide (FeS) precipitates.

These three conditions are met in some soils of Senegal :
1) mangrove soils in tidal swamps ; such soils are found along the western coast of Africa, from Senegal to Cameroon.
Before managing they are high in sulphates and fresh organic matter and very reduced. Sulphate reduction in such soils have been described by HART (1963) VIEILLEFON (1969) and BALDENSPERGER (1969).

2) acide sulphate soils on marine and estuarine sediments high in pyrites and iron monosulphides as on the Senegal River delta.

This paper presents the results of some experiments suggesting that when these soils are reclaimed for rice cultivation, sulphate-reduction may appear not only on the reduced soil as described by TANAKA et al (1968) but first, and very quickly around the germinating seeds and along the roots. Free hydrogen sulphide, and iron monosulphides produced in the spermosphere cause the death of seeds, and in the rhizosphere, the wilting and the death of seedlings. On previous reports (JACQ 1969-1971) we have described similar deleterious processes in the spermosphere and the rhizosphere of maize on waterlogged saline soil in Tunisia.

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D A K A R (SENEGAL)

A) IN SITU OBSERVATIONS

Two types of deleterious phenomena have been observed in situ in some experimental stations on Senegal River delta.

1) Dying out germinating seeds

When heavy rains caused the waterlogging of soil surface during the week following the sowing, seeds may be covered by a blac sheath of iron monosulphide strictly localized in the spermosphere, and produced by sulphate-reducing bacteria. All the seeds died out in a few days as it was observed in Kassak-Nord station last year, in a moderate saline acid sulphate soil (pH : 5.5 ; sulphate content 2.02 me/100g) where leaching is very slow because clay content reaches about 70%.

2) Wilting and dying out of seedlings

In waterlogged areas, where flooding was caused by rains or inadequate leaching of irrigation water, at the beginning of bright periods following cloudy ones, symptoms of disease appeared on rice seedlings: first order leaves, then all the leaves, wilted and dried. Roots were covered by the same black sheath. If sulphide accumulation is important, seedlings died out about 10 days after the manifestation of the first symptoms. Such disease has been ver important is Kassak-Nord soils, less important in Boundoum-Nord soils ($SO_4^=$:1.5 me/100g ; clays : 60%) and Kassak-Sud soils ($SO_4^=$: 0.77 me/100g ; clays : 57%), where pH is higher: 6.0 to 6.4.

B) EXPERIMENTAL STUDIES

1) Material and methods

a) Experiments on soils

Freshly collected samples of mangrove or paddy soils, air-dried and sieved to 2 mm were distributed into flat and transparent colums (50x15x100 mm) described by DOMMERGUES et al (1969). Seeds of rice (IR8 variety) were sown in dry soils. For spermospherical sulphate-reduction studies soils were waterlogged immediatly after the sowing. For rhizospherical sulphate-reduction studies, soils were waterlogged after the seedlings were about 10 cm high. Sulphate-reducing bacteria were enumerated according to STARKEY, reported by PICHINOTY (1966).

b) Experiments on hydroponic cultures

On large test-tubes (JACQ 1971) rice hydroponic axenic cultures were obtained on JACQUINOT's (1968) or BÖRNER and RODEMACHER's (CHALVIGNAC 1958) mineral media. In some experiments an inoculate of sulphate-reducing bacteria was injected into the medium and sulphide content was periodically measured according to CHAUDHRY and CORNFIELD (1966).

Roots exsudates were indentified by paper chromatography and dissolved oxygen partial pressure (pO_2) was measured with a RADIOMETER Blood Micro System analyzer.

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2) Experimentals results

I. SPERMOSPHERICAL AND RHIZOSPHERICAL SULPHATE-REDUCTIONS IN SOME SOILS OF SENEGAL : LABORATORY EXPERIMENTS.

a) Sulphate-reductions in mangrove soils of Casamance.

Mangrove soils of Balingore station (Casamance, South of Senegal) have been described by VIEILLEFON (1969). In table 1 are reported some chemical and physical properties of these soils and th results of sulphate-reducing bacteria enumerations at the middle of dry season (february) and of rainy season (august).

Those numerations showed that sulphate-reducing bacteria are very numerous, more than 1000 cells per g of dry soil, during the whole year on the soils, and present in waters during rainy season.

On flat columns experiments, when IR8 rice was sown and soil immediatly waterlogged, the number of sulphate-reducing bacteria increase rapidly in spermospherical soil (table 2) and on seeds appeared the black sheath of iron monosulphide. A very large part of seeds died out in 8 ot 10 days : from 63% in bare "tanne" soil to 100% in a rhizophora mangrove soil (table 3).

The increase of the number of sulphate-reducing bacteria was slower around roots of survival seedlings (table 2) but all plants were damaged. Only a few of them died out : 23% in bare "tanne" soil and 30% in rhizophora mangrove soil (table 3). After spermospherical and rhizospherical sulphate-reduction the number of survival seedlings (at the 25th day) is low, less than 27% (table 3), even in the mangrove paddy soil.

b) Sulphate reductions in two paddy soils of Casamance and influence of deepness of sowing, waterlogging and

Samples were taken from two paddy soils of Casamance. The clay content and pH (fresh soil) of these soils were respectively:
49.8% and 5.0 for Bignona mangrove saline soil
31.5% and 6.0 for Djibelor, irrigated, non-saline, soil.

In flat columns experiments, 4 Treatments have been differenciated.

(1) Rice seeds sown at 0-1 cm deep ; waterlogged soil
(2) Rice seeds sown at 0-1 cm deep ; flooded soil (water level at 3 cm above soil surface)
(3) Rice seeds sown at 3-4 cm deep ; waterlogged soil.
(4) Rice seeds sown at 3-4 cm deep ; flooded soil.

- Results are reported in table 4 : Spermospherical and rhizospherical sulphate-reductions were always very important when seeds have been deeply sown : in both soils, 40 to 90% of them died out, and half or more of the seedlings too.

When seeds have been sown into the 0-1 cm horizon, spermospherical sulphate-reduction was less important, especially in Bignona soil, but in flooded soils, the number of dead seeds were twice more important than in waterlogged soils, because rhizosphe-

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rical sulphate -reduction, about 25 to 30% of the seedlings died out, excepting in waterlogged Bignona soil (59%).

1) Sulphate-reductions in some different paddy soils

Fourteen paddy soils have been tested : seven mangrove paddy soils, four irrigated soils and three acid sulphate paddy soils.
In table 5 are reported some chemical and physical properties of these soils, and results of flat columns experiments.

Spermospherical sulphate reduction occured only in some mangrove paddy soils. It can be noticed that the two soils where all seeds died out (Balingore and Medina 3) were very saline and clayey, and have been managed last year. In three other soils, the loss of seeds were up to 50 %. In sandy mangrove soil, as Enampar soil, no spermospherical sulphate reduction was observed.

Rhizospherical sulphate-reduction was observed in the fourteen tested soils, but damage caused was important only in Medina 3 mangrove paddy soil, where all the seedling died out, and in two or the mangrove soils where growth of seedlings was very slow. In these three soils, number of sulphate-reducing bacteria might have increased because previous spermospherical sulphate-reduction.

In a non- saline soil (Djibelor 4) and in a acid sulphate soil (Ross-Bethio) rhizospherical sulphate-reduction appeared only at the end of the experiment (two months after sowing) and no plant died out.

II RHIZOSPHERICAL SULPHATE-REDUCTION IN HYDROPONIC CULTURES

a) Inoculation of rice rhizosphere by pure strains of sulphate-reducing bacteria.

In four experiments rice hydroponic axenic cultures were inoculated by pure strains of Desulfovibrio desulfuricans (Hildenborough) or Desulfovibrio gigas. Results are reported on table 6.

Numbers of sulphate-reducing bacteria increased after the 4th day, while a sheath of iron sulphide appeared on the roots, then medium became grey or black. Growth of affected plants have been stunted, and before 10 days, some of them died out. In each test-tube the number of died plants were correlated with the number of sulphate reducing bacteria and with the sulphide content per ml of medium : seedlings died out when sulphide content reaches about $1 \times 10^{-6} S^{=}$ per ml (which is surely lower than sulphide content in the rhizospherical sheath).

b) Inoculation of rice rhizosphere by impure strains of sulphate reducing bacteria.

Impure strains of sulphate-reducing bacteria were obtained on PICHINOTY's medium, from mangrove and paddy soils of Balingore station ; and rice hydroponic axenic cultures, 7 days old, were inoculated by them. Results of periodic enumerations are reported in table: 7.

When initial inoculum was sufficient, rhizospherical sulphate reduction occured, on same manner than with pure strains of sulphate-reducing bacteria, but more slowly. With impures strains from rhizophora mangrove death of seedlings accured in 19 days and with two other strains (from mangrove paddy soil and non-saline heliocharis tanne) growth of rice was affected. When initial inoculum were slight, the number of sulphate-reducing bacteria decreased and iron-sulphide was not observed around roots.

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III RICE ROOT EXSUDATES

It is known that only a few substrates can be utilized as carbon sources by sulphate-reducing bacteria. Such substrates have been identified by paper chromatography (see, table 8, results of amino-acids, aliphatic acids and sugars identifications in IR8 exsudates).

Two aliphatic acids are immediatly available : lactate (STARKEY 1938, SENEZ 1954) and succinate (GROSSMAN and POSTGATE 2953). When amounts of such aliphatic acids are insufficient, some amino-acids may be utilized (MAC PHERSON and MILLER 1962) specially aspartic acid, glutamic acid, asparagine, histidine and threonine, and some sugars, as sucrose, glucose and fructose.

IV OXYGEN DIFFUSION FROM RICE ROOTS

Oxygen partial pressure has been periodically measured with the Radiometer analyzer, in hydroponic media, where 8 plants of rice per test-tube were growing. Results are reported on table 9 : oxygen production by rice roots appeared after 6 or 10 days of incubation in glass-house.

C) CONCLUSIONS AND DISCUSSION

The results summarized here show that sulphate-reducing bacteria are present in two different paddy soils, managed on former mangrove soils or on fluvial estuarine deposits. They may induce, only when strict anaerobiosis is established by waterlogging, the death of rice seeds and seedlings. Heavy rains, or insufficient leaching of irrigation water are main cause of waterlogging, especially when these soils are very clayey and compacted; Such diseases may occur in saline paddy soils, or when brackish water are used in irrigation, because numerous strains of sulphate-reducing bacteria tolerates high sodium chloride contents (LEBAN et al 1966).

Sulphate-reduction appears in whole profile as described by many Japanese searchers (MITSUI et al 1954, YAMADA and OTA 1958, TAKAI and KAMURA 1966) but it appears too, and more quickly, in spermosphere and rhizosphere where available substrates are exsudated. Spermospherical sulphate-reduction, is more intense in the seed than in the root neighbourhood, likely because exsudate production of seed is more important than the exsudate production of roots, and because seeds have not the oxidative power of roots. It can be noticed that light intensity influences the qualitative nature of roots exsudates (ROVIRA 1956) and so, rhizospherical sulphate-reduction is more intense under bright sunshine (JACQ and DOMMERGUES 1971).

As far as we know, no searcher has noticed the death of rice seads because production of sulphides in the spermosphere. But toxicity of the hydrogen sulphide for rice plant is well known : it is toxic at low concentration because its inhibits the respiration, retards the uptake of water and various elements, phosphorus and nitrogen for instance (YAMADA and OTA 1958), and destroys the oxidising power of the roots (TANAKA et al 1968). Thus, without have noticed rhizospherical localization of the injury, many searchers have pointed out the influence of hydrogen sulphide in some rice diseases : "bruzone" (VAMOS 1958, 1959) in Hungary, "root-rot" (BABA 1955) "akiochi" in Japan and Korea and "bronzing" in Ceylon. Akiochi, attributed to

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hydrogen toxicity (PARK and TANAKA 1968, TANAKA and YOSHIDA 1970) occured in degraded soils, low in active iron quite different of acid sulphate soils. In bronzing disease, which may occur in very acid sulphate soils, initial damage by free hydrogen sulphide have destroye the power of the roots to protect plant from excess uptake or iron (TANAKA et al 1968) and made it susceptible to iron toxicity described by PONNAMPERUMA et al (1955). We have shown than in hydroponic cultures when total sulphides content (free hydrogen sulphide and iron monosulphide) reaches 3 or 4 ppm. all plants died out. Perhaps when reduced iron is sufficient to react with all free hydrogen sulphide produced in the rhizosphère it is the iron sulphide sheath which prevent the uptake of some nutrients. Methyl mercaptan, very toxic too, can also be produced by sulphate-reducing bacteria (TAKAI and ASAMI 1962). In acid sulphate paddy soils it is possible that sulphate reductions occur more easily when plants have yet suffered from any other toxicity or any element deficiency. For instance salinity is usually associated with acidity on such coastal areas. If spermospherical sulphate-reduction is not promoted by salinity toxicity, because germinating seeds are most tolerant to salinity, rhizospherical sulphate-reduction may be more important in saline acid sulphate soil, especialy et seedling stage, when plants are very sensitive. After this stage, the oxidative power of rice roots (AIMI 1960, BARBER et al 1965, ARMSTRONG 1969, LUXMORE et al 1970), may oxidise iron monosulphide seath and reduce its toxicity; we have noticed it in preliminary test-tube experiments and field observations show that when plants have been little injured, disease symptomes disappeared and the growth of survivals plants is better than the growth of non-affected plants .

Not only rice, but many plants may be affected by spermospherical and rhizospherical sulphate-reduction : Fields observations (DOMMERGUES et al 1969) and preliminary experiments (JACQ 1969) on a saline soil from Tunisia, show that some plants are very susceptible : legumes (french bean, broad bean, lucerne) and cereals (maïze, sorghum). In Senegal, cotton and sugarcane may be also damaged. The study of the effects of these processes is of a reel pratical interest every time sulphated soils may be waterlogged after sowing or during growth of such susceptible plants.

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TABLE 1 : SOME CHEMICAL AND PHYSICAL PROPERTIES OF MANGROVE AND PADDY SOILS OF CASAMANCE ENUMERATIONS OF SULPHATE REDUCING BACTERIA IN THESE SOILS.

SOIL	CHEMICAL AND PHYSICAL PROPERTIES						$\log_{10}$ of number of sulphate reducers /g of dry soil or ml of water.		
	Clay (2µm) x 10^{-2}	Carbon x 10^{-2}	C/N	pH	$SO_4^=$ me. per 100 g	Cl^- me. per 100 g	Soil in dry season	Soil in rainy season	Water in rainy season
Rhizophora mangrove	80.6	13.2	86.5	6.2	4.9	55.6	4.56	4.23	2.47
Avicenia mangrove	78.1	2.2	19.2	6.2	1.3	26.5	-	4.82	1.47
Bare and saline "tanne"	66.1	2.2	23.9	4.8	6.2	67.7	3.53	3.23	1.78
Heliocharis saline "tanne"	76.7	1.4	12.0	5.0	10.8	53.4	-	2.92	1.81
Heliocharis non-saline "tanne"	73.1	1.5	13.7	5.8	7.0	-	3.57	5.94	1.45
Mangrove paddy soil	-	-	-	-	-	-	4.32	3.61	2.90

TABLE 2 : ENUMERATIONS OF SULPHATE REDUCING BACTERIA IN THE SPERMOSPHERE AND THE RHIZOSPHERE OF IR8 RICE SOWN ON SOME WATERLOGGED MANGROVE AND PADDY SOILS.

S O I L	Number of sulphate-reducing bacteria per g. of dry soil (log_{10})						
	In soil	In Spermospherical soil			In Rhizospherical soil		
	Day = 0	8	15	22	12	19	25
Rhizophora mangrove	4.27	5.60	4.53	6.29	-	3.14	6.39
"	3.68	3.80	3.96	-	-	-	-
Avicenia mangrove	3.59	4.13	-	6.80	2.62	3.66	-
"	3.36	5.61	3.01	5.14	3.52	-	-
Bare and saline "tanne"	2.50	3.35	4.00	5.06	5.49	5.38	6.46
Heliocharis saline "tanne"	2.88	3.72	3.24	5.17	3.10	-	-
Heliocharis non-saline "tanne"	2.31	4.50	3.70	6.66	-	7.02	-
Mangrove paddy soil	4.41	5.38	3.72	5.13	5.62	3.63	8.64

TABLE 3 : IR8 RICE SEEDS DIED OUT BY SPERMOSPHERICAL SULPHATE-REDUCTION AND IR8 RICE SEEDLINGS DIED OUT BY RHIZOSPHERICAL SULPHATE-REDUCTION IN SOME MANGROVE AND PADDY SOILS.

SOIL	PERCENTAGES			
	(A) SEEDS DIED OUT	(B) SEEDLINGS AFFECTED	(C) SEEDLINGS DIED OUT	(D) SURVIVAL SEEDLINGS (25th day)
Rhizophora mangrove	87	100	30	10
"	100	-	-	0
Avicenia mangrove	90	100	0	10
"	90	100	0	10
Bare and saline "tanne"	63	92	23	27
Heliocharis saline "tanne"	95	100	0	5
Heliocharis non-saline "tanne"	97	100	0	3
Mangrove paddy soil	77	100	0	23

TABLE 4 : I.R.8 RICE SEEDS AND SEEDLINGS DIED OUT BY SPERMOSPHERICAL AND RHIZOSPHERICAL SULPHATE REDUCTIONS IN TWO PADDY SOILS : INFLUENCE OF DEEPNESS OF SOWING AND WATERLOGGING.

S O I L	DEEPNESS OF SOWING	PERCENTAGE OF PLANTS DIED OUT BY				SURVIVAL SEEDLINGS (%)	
		SPERMOSPHERICAL SULPHATE-REDUCTION		RHIZOSPHERICAL SULPHATE-REDUCTION		in waterlogged soil	in flooded soil
		waterlogged soil	flooded soil	waterlogged soil	flooded soil		
BIGNONA paddy soil	surface sowing (0-1 cm)	9	15	59	23	38	66
	deep sowing (3-4 cm)	90	95	50	40	5	3
DJIBELOR paddy soil	surface sowing (0-1 cm)	44	80	28	24	41	16
	deep sowing (3-4 cm)	98	98	50	100	1	0

TABLE 5 : SULPHATE-REDUCTION IN THE SPERMOSPHERE AND THE RHIZOSPHERE OF IR8 RICE ON SOME PADDY SOILS.

SOILS		SOME PHYSICAL AND CHEMICAL PROPERTIES					SULPHATE-REDUCTION		
Experimental stations		pH	Clays %	Organic matter °/oo	C/N	Cl^- me. / 100 g	Spermospherical	Rhizospherical	Growth of Rice
MANGROVE PADDY SOILS (CASAMANCE)	BALINGORE	6.2	45.0	13.0	40	28.7	Very important	-	seeds died out
	MEDINA 1	4.0	66.0	29.6	28	13.4	important	important	weak
	MEDINA 2	4.3	27.5	155	29	23.0	important	important	seedlings died out
	MEDINA 3	4.2	65.8	19.4	19	42.9	Very important	-	seedlings died out
	MEDINA 4	4.5	35.8	127	25	40.1	none	low	good
	BIGNONA	5.0	49.8	48.9	14	3.7	low	important	weak
	ENAMPAR	6.3	25.5	27.6	20	13.5	none	low	good
NON-SALINE PADDY SOILS	DJIBELOR 1	6.2	21.0	40.1	16	4.13	none	low	good
	DJIBELOR 2	6.1	15.8	56.8	13	0	none	low	good
	DJIBELOR 3	6.1	13.0	11.8	15	0	none	low	good
	DJIBELOR 4	6.0	31.5	68.0	13	0	none	very important	good
PADDY SOIL IN SENEGAL DELTA	ROSS-BETHIO	4.6	60.5	23.0	18	1.2	none	very important	good
	BOUNDOUM	6.3	47.7	23.2	23	0.9	none	low	good
	RICHARD-TOLL	5.4	34.8	12.0	12	0.6	none	low	good

TABLE 6 : RHIZOSPHERICAL SULPHATE-REDUCTION IN RICE HYDROPONIC CULTURES INOCULATED BY PURE STRAINS OF SULPHATE REDUCING BACTERIA.

INOCULUM 5 ml of liquid culture	Experiment	Experimental conditions	Number of sulphate reducing bacteria / ml (log_{10})			Sulfide content: $10^{-6}S^{=}$/ ml of medium (10th day)	Seedlings died out at the 10th day (per cent)
			Inoculation day -	4 days later	8 days later		
Desulfovibrio desulfuricans (Hildenborough)	A	12 days old seedlings 6000 lx 28°C	3.85	2.78	4.85	-	10
	B_1	5 days old seedlings in glasshouse (20-32°C)	3.47	2.60	3.47	0.89	0
	B_2		3.76	2.88	6.60	1.37	40
	B_3		4.03	4.78	8.34	7.12	100
Desulfovibrio gigas	C	12 days old seedlings 6000 lx 28°C	3.36	2.90	4.34	-	100
	D_1	16 days old seedlings in glasshouse (22-35°C)	4.66	4.36	6.65	3.10	30
	D_2		5.60	5.38	6.85	5.97	80

TABLE 7 : RHIZOSPHERICAL SULPHATE-REDUCTION IN RICE HYDROPONIC CULTURES INOCULATED BY SULPHATE-REDUCING BACTERIA OF SOME MANGROVE AND PADDY SOILS.

INOCULUM 5 ml of impure strain from	Number of sulphate-reducing bacteria (log_{10})/ml of hydroponic culture					Rhizospherical Sulphate-reduction	Growth of IR8 rice seedlings
	Inoculation day	4 days later	7 days later	12 days later	19 days later		
Rhizophora mangrove soil	2.04	1.15	1.48	2.36	2.43	low	weak
	4.76	2.60	3.48	3.86	4.34	very important	seedlings died out
Avicenia mangrove soil	2.60	2.48	1.90	1.48	1.08	none	good
Bare and saline "tanne" soil	1.04	1.48	1.26	1.95	1.60	none	good
	4.53	2.70	2.48	2.60	2.48	low	weak
Non-saline Heliocharis "tanne" soil	1.08	1.26	2.36	1.48	1.48	none	good
	2.78	1.34	3.34	3.28	4.18	very important	weak
Mangrove paddy soil	2.36	1.26	1.95	2.48	2.90	low	weak
	3.45	1.60	2.78	2.90	3.85	important	very weak

TABLE 8 : ROOT EXSUDATES OF IR8 RICE.

Amino-acids	RC (*)		RC	Aliphatic acids	RC	Sugars	RC
leucine	3	glutamic acid	3	quinate	2	raffinose	3
isoleucine	1	serine	3	tartrate	3	maltose	0
β-alanine	0	citrulline	5	oxalate	3	sucrose	2
tryptophane	0	glycine	3	citrate	2	galactose	1
valine	1	aspartic acid	4	malate	0	glucose	3
méthionine	$\pm$	arginine	4	lactate	1	fructose	3
tyrosine	0	asparagine	3	malonate	$\pm$	arabinose	0
proline	3	histidine	3	succinate	1	xylose	0
cystéine	$\pm$	lysine	4	fumarate	0	ribose	1
α-alanine	2	cystine	0			rhamnose	0
thréonine	2						

(*) RC : relative concentration.

TABLE 9 : OXYGEN DIFFUSION FROM ROOTS OF IR8 RICE INTO THREE HYDROPONIC AXENIC CULTURE MEDIA.

HYDROPONIC MEDIA AND INITIAL pH	Age of plants (in days)	Dissolved oxygen partial pressure (PO_2) in mm Hg.		
		Control (no plant) C (*)	Rice hydroponic culture R (*)	R-C
BORNER-RÖDEMACHER pH 6.5	2	139	139	0
	7	151	145	- 6
	10	154	158	+ 4
BORNER-RÖDEMACHER pH 4.5	1	161	160	- 1
	6	162	167	+ 5
	11	152	181	+ 29
	18	150	178	+ 28
JACQUINOT pH 6.0	1	160	157	- 3
	6	155	154	- 1
	11	160	174	+ 14
	18	157	170	+ 13

(*) average of 6 measurements, 5 plants per test-tube.