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Effects of Salinity on Leaf Growth and Photosynthesis in Rice**

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鹽處理가 水稻잎의 伸長 및 光合成能에 미치는 影響**

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ABSTRACT : The studies aimed to distinguish between initial (ionic or osmotic) effects of salinisation on growth and the longer-term consequences of excessive salt accumulation. Tall and dwarf varieties of rice were used to provide different growth rates. There was no significant effect upon the day-to-day pattern of growth, upon the ultimate length of leaves that were developing at the time of, or shortly after, salinisation with 50 mM NaCl. Leaves that developed after prolonged exposure of the plants to salinity were shorter. Addition of NaCl, KCl or *mannitol* to the root medium brought about a cessation of leaf elongation within one minute. Growth at a reduced rate restarted abruptly after a lag period that depended upon the external concentration. Elongation rate recovered to its original value within 24 hours after exposure to 50 mM NaCl, though not at higher concentrations.

Addition of NaCl at concentrations up to 100 mM elicited no short-term effect upon photsynthetic gas exchange. No change in turgor pressure was detectable in the growing zone with the resolution of the miniature pressure probe used (about 70 kPa). It is concluded that the initial growth reduction in rice caused by salinisation is due to a limitation of water supply. A clear distinction is made between the initial effects of salt which are recoverable, and the long-term effects which result from the accumulation of salt within expanded leaves.

INTRODUCTION

Rice belongs to the genus *Oryza*, which consists mostly of perennial species native to freshwater swamps and marshes (Oka, 1988). The species is sensitive to salinity, concentration of NaCl as low as 50 mM causing a range of mortality according to variety, when applied at the seedling stage (Yeo et al., 1990). In rice, large quantities of salt are carried to the leaves in the transpiration stream, which leads eventually to their sequential death. It is known that NaCl accumulation in the leaves is correlated with reduced photosynthetic activity and with ultrasructural and metabolic damage (Yeo and Flowers, 1986, 1989), and that, in the long term, this is mediated by apoplastic salt accumulation in the expanded leaves (Flowers et al., 1991). The influx of salt with the transpiration stream, amplified by the distribution between apoplast and protoplast, accounts for the long-term toxicity of even low external salinities.

There is much variability in salt susceptibility both between and within varieties ; differences in vigour accounting for much of the variation in the survival of salinity (Yeo et al., 1990). A reduction in growth by salinity is liable, therefore, to lead to positive feedback, and the maintenance of growth in the presence of salinity is consequently vital. I do not, however, know whether there is any initial effect of salinisation upon growth processes, or whether damage develops only as a consequence of excessive salt uptake. There has been much debate as to whether water deficit,

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specific ion toxicity or other process is responsible for salt damage, and whether the site of action is expanded or expanding cells (see, for example, Munns and Termaat, 1986), but it has proven difficult to generalise.

The studies aimed to investigate the effects of salinity upon the growth of leaves in tall and dwarf varieties of rice, and specifically to separate short and long-term effects of salinisation.

MATERIALS AND METHODS

Plant Material

Seeds of rice (*Oryza sativa* L.) were obtained from the International Rice Research Institute, Philippines and from Dr. M. Al-Azawi in Iraq. The elite breeding lines IR 2153-26-3-5-2 and IR 4630-22-2-5-1-3 are dwarf. Pokkali is a tall traditional landrace and the Iraqi variety Amber is of intermediate stature. Amongst species, rice is at the sensitive end of the salt tolerance spectrum. Amongst rice varieties, Pokkali and IR 4630 are salt resistant and Amber and IR 2153 are moderately resistant. Sensitive varieties were not included because too many individuals die before any useful measurements can be made. In the majority of experiments IR 2153 and Pokkali were used as representatives of the dwarf and tall groups. In the long-term glasshouse experiments Amber was used in place of Pokkali because the very long leaves of the latter were too easily damaged during the handling necessary to measure the lengths of all the leaves.

Leaf Initiation, Leaf Death and Ultimate Leaf Length

Three varieties, IR 2153, IR 4630 and Amber were used. Seed was germinated and grown as detailed by Yeo et al (1990). The culture solution was modified (by reducing the phosphate concentration by half) from that of Yoshida et al (1976). The experiments were carried out during March and April during which time the glasshouse was heated to a minimum of 25℃ by day and 20℃ by night and supplementary lighting gave a minmum of 300 umol m^{-2} s^{-1} photosynthetically active radiation for 12 hr per day. The temperature range was up to 30℃ and the light intensity up to 1000 umol m^{-2} s^{-1}. Daytime humidity was between 60 and 80%.

Seedlings age 7 days were transplanted into black-painted plastic boxes and salt treatments were salinised with 50 mM NaCl on day 15. Twenty plants per variety were used in control treatments and, because of the high variability under saline conditions (Flowers and Yeo, 1981), 60 plants per variety were used in NaCl treatments. Leaf emergence and leaf death were recorded daily and leaf length every 2 or 3 days. Measurements were terminated on day 42 when plant mortality in the salinity treatments became substantial.

Leaf Growth Measurements

Seedlings of Pokkali and IR 2153 were transplanted at 7 days into individual "Pyrex" tubes of 50cm^3 capacity wrapped in aluminium foil to exclude light from the root medium. They were grown in a controlled temperature room at 25℃ with light provided for 12 hr per day at 300 umol m^{-2} s^{-1} photosynthetically active radiation (Wotan HQ-1). The lengths of each leaf on each plant was measured daily.

For continuous monitoring of leaf growth, plants were transferred to glass containers fitted with a tap to enable rapid replacement of the nutrient solution. The leaf to be investigated was connected to a displacement transducer (Sangamo SM3, RS Components Ltd) by nylon monofilament fishing-line (0.117 mm diameter) passing over a pulley made of solid PTFE. The force on the leaf was 1.2g. The displacement transducer was mounted in a micromanipulator to allow centralisation of the unguided core and the frequent adjustment of the transducer body with leaf growth (as the linear range was only some 1.5 mm). The apparatus was damped against vibration by mounting on a heavy steel plate seated on an airtube. The plant was illuminated (350 umol m^{-2} s^{-1}, Wotan HQ-1) via a heat-shield of twin-wall polycarbonate to minimise thermal effects. Plants were used at a time in which the measured leaf was undergoing uniform daily growth increments. After a linear extension rate was obtained in culture solution, the solution was rapidly replaced by NaCl, KCl or mannitol (at the osmotic equivalent of 50 mM NaCl).

After growth had resumed at a new rate, the external medium was increased by another 50 mM NaCl or

the equivalent, and so on up to 150 mM NaCl. At each step, extension rates, and the lag-time before extension growth resumed, were recorded. To determine the effect of experimental handling, a series of controls was performed in which culture solution was replaced by culture solution. In a separate set of experiments, the growth rate of leaves was measured before, and again 6 and 24 hr after, salinisation with 50, 100 and 150 mM NaCl.

Gas Exchange Measurements

Measurements were made in a open system as described by Yeo et al (1985). Air with regulated vapour pressure deficit passed over single leaves in leaf chambers constructed of "Perspex" and water vapour and carbon dioxide concentrations determined with a dew-point meter(EG & G model 911) and infrared gas analyser (ADC model 225). Calculation of stomatal conductance and intercellular carbon dioxide concentration were made according to Jarvis (1971). The experimental regime was similar to that for the growth measurements in that plants were exposed to a stepwise increase in NaCl(or the equivalent mannitol) concentration over the course of a day such that new steady rates were obtained at each increment.

Leaf Water Potential Measurements

An intact leaf chamber (model C52, Wescor Inc.) was attached to an expanded leaf with the plant in a glass container fitted with a tap. The leaf chamber output was measured with a microvoltmeter (model HR33T, Wescor Inc.) at intervals while the concentration of the external medium was changed in steps of 50mM NaCl.

Turgor Pressure Measurement

Individual cell turgor pressures were recorded using the pressure-probe technique described by Husken et al (1978). A microcapillary (tip diameter 1-2 um) and pressure transducer (Druck Ltd., Leicester, UK) were mounted in a custom-built Perspex block. The system was calibrated using roots of the halophyte *Suaeda maritima*. The smallest change in external concentration (in the flowing solution bathing the roots) that gave a detectable change during continuous recording of the turgor of an epidermal cell was 15 mM NaCl. This is equivalent to a resolution of about 70 kPa.

RESULTS

Leaf Survival

The survival of leaves in both salinised and unsalinised populations followed two phases(Fig. 1.). There was an initial period of low mortality (a half -life of about 10 days for leaves 1, 2 and 3) which changed abruptly (at different sequential times for each leaf) to a very rapid senescence phase with a half -time of less than 2 days. The rates of both phases in the presence and absence of salt were quite similar, as they were for the three different leaves. The rapid

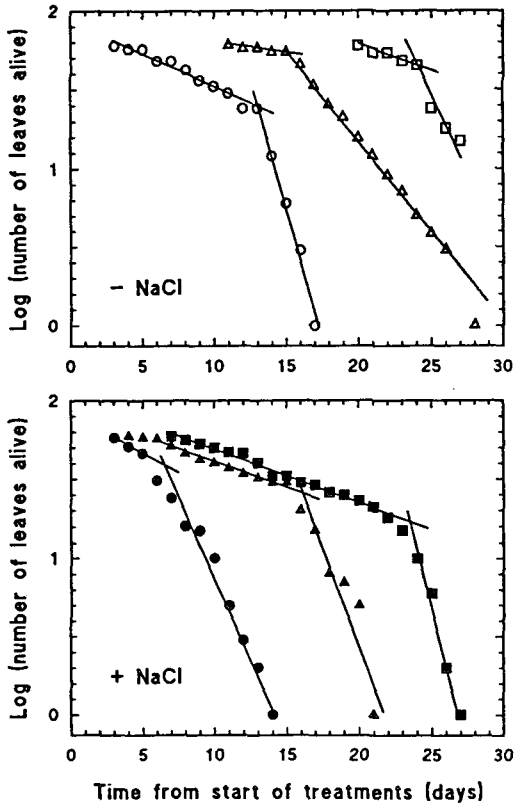

Fig. 1. Survival of different leaves in *Oryza sativa* L. elite breeding line IR4630-22-2-5-1-3 with and without the addition of 50 mM NaCl to the culture solution on day 15. Circles, leaf 1; triangles, leaf 2; squares, leaf 3

Table 1. *Leaf emergence in three varieties in the presence and absence of* 50 *mM NaCl*. Plants were grown in a glasshouse and salt was added on day 15.

Variety	Leaf	Day of emergence		Delay caused by NaCl	1	2	3
		0 NaCl	mM NaCl				
IR 4630	4	14.7±0.7	15.3±1.0	0.6	59		
	5	19.2±0.8	20.2±1.2	1.0	59		
	6	24.6±0.8	26.1±1.6	1.5	58	1	
	7	30.3±0.9	31.7±1.5	1.4	54	5	
	8	35.7±1.0	38.0±1.5	2.3	48	8	3
IR 2153	4	16.4±0.5	16.6±0.7	0.2	60		
	5	20.8±0.6	21.8±1.3	1.0	58	2	
	6	26.2±0.8	27.9±1.7	1.7	56	4	
	7	32.0±1.0	33.2±1.4	1.2	34	26	
	8	38.0±1.2	38.9±1.3	0.9	23	32	5
Amber	4	17.9±0.8	18.2±0.9	0.3	60		
	5	23.0±1.0	23.5±1.0	0.5	60		
	6	27.9±1.0	29.4±1.2	1.5	60		
	7	32.5±0.8	34.6±1.7	2.1	59	1	
	8	38.2±1.4	40.0±1.1	1.8	46	11	3

Mean and standard deviation
For 0 mM NaCl n=20
For 50 mM NaCl :
[1] number of plants from which the mean is obtained (n)
[2] number of plants from the population which had died before the leaf emerged.
[3] number of plants which were alive, but in which the leaf had hot emerged by day 42.

senescence phase was initiated earlier in the salinised population of leaves. The first phase of mortality also began earlier and accounted for a higher proportion of leaf mortality in the salinised than in the unsalinised population.

There was little effect of salt upon leaf emergence ; delays were only about one or two days (Table 1). Even though more than 50% of plants in the IR 2153 population had died before leaf 8 emerged ; the delay in emergence in those plants remaining alive was only 0.9 days (NS). The principal effect of salinity was to bring about premature leaf senescence (Table 2, 3, Fig. 1). Thus the useful photosynthetic life of the leaf was severely curtailed.

Ultimate Leaf Length

There was very little effect of 50 mM NaCl upon the length of leaves which developed soon after salinisation. Although the leaves of the non-dwarf Pokkali are some 2.5 times as long as in IR 2153, the pattern of growth of the early leaves was very similar between the varieties (Fig. 2.), and there was only a marginal reduction in the ultimate length of leaf 3 in Pokkali (Table 4). When plants were grown for longer in the glasshouse, reduced leaf size in the salinised treatments became significant only in leaves that developed after prolonged exposure of the plants to salt (Table 5).

Leaf Elongation Rates

When the culture solution surrounding the root was drained and replaced, elongation rate, measured with the transducer, stopped within one minute. After a brief lag (of less than 2 minutes) elongation resumed at a rate identical to that before. Following replacement with a culture solution with addition of NaCl, KCl or mannitol there followed a period of zero elongation (lasting about 20 minutes for IR 2153 at low concentrations of KCl and NaCl) after which elongation resumed abruptly (Fig. 3). The length of this lag phase increased with concentration (Fig. 4).

The elongation rate which developed after the lag was reduced in both varieties by about 35% in 50 mM NaCl and by 70% in 150 mM NaCl. In IR 2153, KCl

Table 2. *Death of leaves that had emerged before salinisation was imposed (leaves 1-3) in three varieties*. Plants were or were not salinised with 50 mM on day 15. Plant age in days. Mean and standard deviation ; n=10 (0mM NaCl) and n=60 (50 mM NaCl).

Variety	Leaf	Leaf death (days from germination)		Loss[a] (days)
		0 m M NaCl	50 mM NaCl	
IR 4630	1	25.0±3.9	21.4±2.7	3.7
	2	32.0±3.5	27.5±4.7	5.0
	3	38.4±1.7	31.6±6.1	7.1
IR 2153	1	24.1±1.4	21.7±2.8	2.5
	2	28.9±2.1	24.2±2.8	3.9
	3	35.6±1.8	28.0±4.0	5.6
Amber	1	32.4±4.5	23.1±2.6	10.4
	2	39.2±2.1	30.5±4.7	9.0
	3	> 42[b]	35.1±4.7	> 7

[a] The loss of life of the different leaves computed from the duration of individual leaves after salinisation as : Sum of (number dying x days alive)/N

[b] Leaf 3 of the variety Amber had not senesced by the end of the 42-day period of observation

was equally inhibitory but equiosmolal mannitol was more inhibitory than the salts (50% inhibition at 100 mM mannitol and 95% at 300mM). The picture was somewhat different with Pokkali, where KCl was more inhibitory than NaCl and equal to mannitol (50% inhibition by 50 mM KCl or 100 mM mannitol) ; Fig. 5. There was close correspondence between the response of the two varieties in terms of elongation rate and lag times. At 300 mM mannitol, some plants did not recover a measurable growth rate. The leaf elongation rate following imposition of 50 mM NaCl was following during the remainder of the photoperiod, and during the photoperiod the following day, for a total of up to 24 hr. The reduction in elongation rate was transient.

Gas Exchange

There were no significant short-term effects of NaCl concentrations up to and including 100 mM on net photosynthesis, transpiration, stomatal conductance or intercellular CO_2 concentration (Table

Table 3. *Proportion of leaves which emerged after day 15 (When the plants were salinised with 50 mM NaCl) that had died by the end of the period of observation (day 42) for three varieties*. The number of plants in which a particular leaf had emerged (n), the proportion of these leaves which were alive or dead at day 42, and the mean survival period of those leaves dying during the period of observation.

Variety	Leaf	n	Dead (%)	Alive (%)	Survival (days)
IR 4630	4	59	78	22	19.0±4.9
	5	59	71	29	16.5±3.1
	6	58	36	64	13.5±2.4
	7	54	8	92	7.3±2.1
	8	48	0	100	–
	9	5	0	100	–
IR 2153	4	60	95	5	16.0±4.8
	5	59	81	19	12.8±3.3
	6	56	66	34	9.5±3.8
	7	34	18	82	6.0±3.0
	8	23	0	100	–
Amber	4	60	80	20	19.4±3.3
	5	60	45	55	16.7±2.1
	6	60	8	92	11.2±4.3
	7	60	3	97	4.5±3.9
	8	46	0	100	–

In control plants, no leaf number 4 or later had died by day 42.

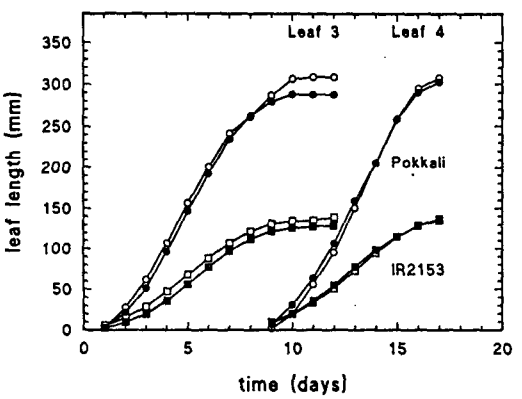

Fig. 2. Leaf length in *Oryza sativa* L. Pokkali (circles) and IR 2153-26-3-5-2 (squares) with and without the addition of 50 mM NaCl. Open Symbols are plants without salt and filled symbols are plants with 50 mM NaCl. Points are mean values ; n=12(leaf 3) and n=9(leaf 4).

Table 4. *Ultimate length of leaves of IR2153 and Pokkali grown with and without the addition of NaCl (50 mM) to the culture solution.* Plants were grown in a controlled temperature room and the timecourse of mean leaf length is shown in Figure 2. Mean and standard deviation ; n=12 (leaf 3) and n=9 (leaf 4).

Variety	NaCl (mM)	Leaf length (mm)	
		Leaf 3	Leaf 4
IR 2153	0	138.8±13.4	136.8±20.4
	50	128.9± 9.5	135.3±19.3
Pokkali	0	308.6±13.1	307.5±12.8
	50	287.8±14.7	302.8± 9.5

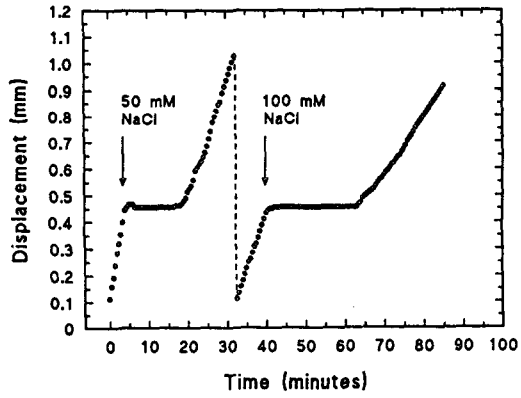

Fig. 3. The timecourse of leaf elongation recorded continuously with a displacement transducer whilst the root medium was replaced with a medium containing first 50 mM NaCl then 100 mM NaCl. Sample traces ; variablity in elongation rates and lag times are given in Figs 4 and 5.

6). Concentrations of 150 and 200 mM NaCl caused substantial reductions in all four parameters. Equiosmolal mannitol was generally more inhibitory than NaCl and there were reductions in transpiration rate and stomatal conductance in 200 mM mannitol although there were none in 100 mM NaCl. In all cases, water loss was reduced by a greater factor than was net photosynthesis such that leaf water-use efficiency increased under water deficit. There was a reduction in the intercellular concentration of CO_2 as the concentration of salt or mannitol in the external root medium was incresed. When plants were returned to culture solution overnight, leaf gas exchange parameters had returned to their values before

Table 5. *Ultimate length of leaves of three rice varieties in the presence and absence of 50 mM NaCl.* Plants were grown in a glasshouse and salt was added on day 15. Leaf 3 emerged before salinisation, leaf 4 emerged (according to variety) at or shortly after salinisation, and subsequent leaves at intervals thereafter of 4-5 days. Exact times of leaf emergence are given in Table 1.

Variety	Leaf	Final leaf length (mm)		%
		0 mM NaCl	50 mM NaCl	
IR 4630	3	123.5± 6.5 (10)	116.7±10.2 (59)	94
	4	160.0±16.1 (10)	149.7±13.7 (59)	94
	5	188.0±10.6 (10)	155.6±20.0 (58)	83
	6	238.8±17.3 (10)	182.1±37.4 (56)	76
	7	257.3±16.6 (10)	192.0±46.8 (54)	76
IR 2153	3	161.9± 7.2 (10)	155.9±10.1 (60)	96
	4	202.3± 7.6 (10)	171.3±19.0 (60)	85
	5	240.6± 9.6 (10)	183.4±33.2 (59)	76
	6	273.2± 8.1 (10)	170.4±75.0 (54)	62
	7	313.7±21.4 (10)	211.9±88.2 (34)	68
Amber	3	260.9±18.0 (10)	263.3±20.1 (60)	101
	4	283.1±17.7 (10)	259.8±19.2 (60)	92
	5	364.7±22.2 (10)	336.9±35.9 (59)	92
	6	416.6±19.6 (9)	357.6±54.1 (49)	86

Mean and standard deviation (n in parenthesis).

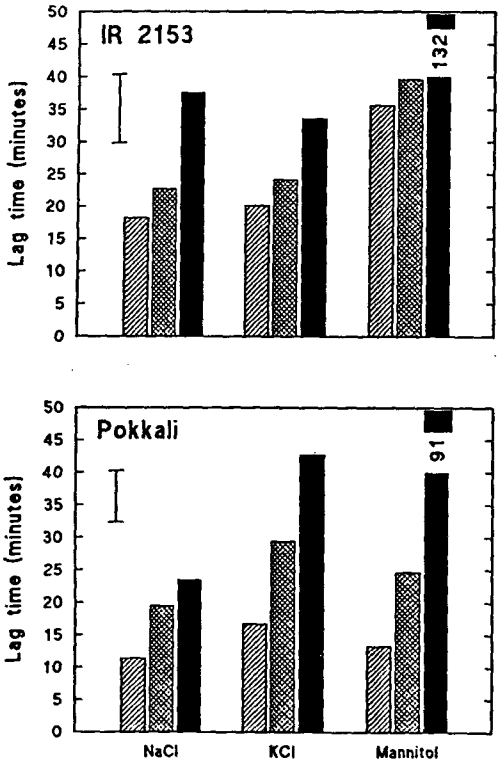

Fig. 4. The lag time before elongation growth recovered in *Oryza sativa* L. Pokkali and IR2153-26-3-5-2 following sequential increases in the concentration of NaCl, KCl or mannitol in the root medium. Single hatching, 50 mM salts or 100 mM mannitol ; cross hatching, 100 mM salts or 200 mM mannitol ; solid bar, 150 mM salts or 300 mM mannitol. The L.S.D. at P=0.05 is shown for each variety.

salinisation commenced by the following day, even when the leaf had become visibly rolled.

Turgor Pressures in the Elongation Region

No change in turgor pressure was detectable within the resolution of the pressure-probe (about 70 kPa) when the external root medium was changed from culture solution to culture solution plus 50 mM NaCl. Microscopical observation revealed only a very small movement of the water/oil meniscus as cells in the rice expansion zone were penetrated.

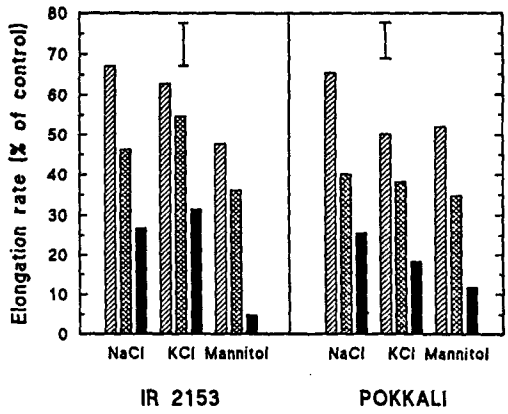

Fig. 5. Leaf elongation rates, measured with a displacement transducer, for *Oryza sativa* L. Pokkali and IR2153-26-3-5-2 following sequential increases in the concentraion of NaCl, KCl or mannitol in the root medium.

DISCUSSION

Short and Long Term Effects of Salinity

The addition of 50 mM NaCl to the culture solution stopped leaf elongation for no more than 20 minutes, after which growth resumed at a new, reduced rate which recovered completely by the following day. There were no short term effects upon any leaf gas exchange parameter. This is in marked contrast with the longer term effects of growing rice plants in 50 mM NaCl, where leaf growth was inhibited, leaf longevity was reduced and substantial plant mortality occurred. The initial response of rice varieties to low salinity are transient and are thus separated clearly from the pathological consequences of exposure to the same level of salinity in the longer term, which are catastrophic. I argue that the first stage is due to reduced water supply to the growing zone and that the longer-term effects are the pathological consequence of continuous, excessive ion uptake.

The Causes of Transient Stoppage of Growth

The growth pattern of stressed leaves was characterised by four phases : an abrupt cessation of elongation growth, a period of zero elongation, an abrupt resumption of elongation growth at a reduced rate, and the gradual recovery (at low, 50 mM NaCl salin-

Table 6. *Gas exchange parameters in individual leaves of two varieties following the addition of various concentrations of NaCl or mannitol to the root medium.* Individual plants were progressively stepped up from culture solution with sequential increments of 50 mM NaCl or 100 mM mannitol over the course of a day. Values for net photosynthesis and transpiration were recorded when they had been steady for at least 30 minutes. Means of four determinations.

Variety/ treatment		P_n ($mg\ CO_2\ m^{-2}\ s^{-1}$)	E ($mg\ H_2O\ m^{-2}\ s^{-1}$)	g CO_2 ($mm\ s^{-1}$)	C_i ($mg\ m^{-3}$)
IR2153					
NaCl	0	0.51	48.0	2.85	400
	50	0.50	49.7	2.97	406
	100	0.50	44.6	2.63	376
	150	0.48	31.2	1.75	290
	200	0.39	16.9	0.91	137
Mannitol	0	0.50	51.9	2.88	405
	100	0.51	51.3	2.85	402
	200	0.49	34.1	1.79	306
	300	0.38	17.9	0.90	149
	400	0.21	8.3	0.41	136
LSD P=0.05		0.04	6.1	0.35	54
Pokkali					
NaCl	0	0.46	41.6	2.30	375
	50	0.46	41.3	2.30	376
	100	0.46	38.9	2.14	362
	150	0.44	29.2	1.81	293
	200	0.37	21.4	1.11	242
Mannitol	0	0.40	42.2	2.26	399
	100	0.40	43.5	2.33	404
	200	0.41	38.2	2.01	362
	300	0.34	18.6	1.39	188
	400	0.21	10.7	0.52	192
LSD P=0.05		0.03	5.6	0.43	53

ity) of the original elongation rate. I agree with Tomos et al (1989) that the timescale makes a direct effect of NaCl upon the walls of the cells of the expanding zone an unlikely explanation. Strong circumstantial evidence in support of this comes from the fact that the high individual variability in NaCl uptake which is normal in rice (Yeo et al., 1988) was not seen in the initial growth responses.

The simplest interpretation is that the lowering of the water potential of the root medium reduced water supply to the leaf. This led to the turgor pressure (P) in the expanding zone falling below the yield threshold (Y) so that growth stopped. The difference between the steady state turgor prior to salinisation and yield threshold must be less than 0.24 MPa since 50 mM NaCl stopped elongation completely and immediately. During the ensuing lag phase it is presumed that osmotic adjustment is taking place. Rice varieties, including lowland types, have been shown to be capable of osmotic adjustment of at least 0.5 MPa in response to water deficit (Hsiao et al., 1984). Osmotic adjustment would restore the gradient in water potential between the vacuoles of the cells of the expansion zone and the external medium, so that turgor again exceeded the yield threshold, and growth resumed. Whether this is mediated by organic synthesis, ion uptake or solute transport from the expanded leaves requires further investigation. There is a sug-

gestion that ion uptake plays some role, because the salts were less inhibitory than mannitol. NaCl and KCl offer a source of osmotically active solutes whilst mannitol, with a high reflection coefficient, does not.

The resumption of growth was abrupt, and the new growth rate, though reduced, was quite stable. The transition from zero elongation to a new elongation rate occurred in a matter of seconds (Fig. 3.) ; a true threshold effect. There was no acceleration, as would be expected if continued osmotic adjustment led to a continued rise in P, and elongation rate was proportional to P-Y. The turgor pressure needed to sustain growth in rice appears, therefore, very close to the yield threshold. Either growth is independent of P above the yield threshold or, as soon as P exceeds Y, cell expansion leads to stress relaxation and to the immediate resumption of a steady-state value for P, close to the yield threshold. The data do not resolve these alternatives.

The behaviour of rice leaf elongation rate conforms most closely to the behaviour expected if wall extensibility is much greater than hydraulic conductance (Cosgrove, 1981). In these circumstances growth is limited by water uptake, the cell expands whenever P>Y, and consequently turgor rests very close to the yield threshold (Cosgrove 1981). This would be consistent with the inability to observe a change in turgor with the pressure-probe, and with the apparent low elasticity of the cells of the expansion zone. This parallels the observations of Tomos et al (1989) with wheat. They also could detect no reduction in P in the expanding cells when leaf elongation rate changed as a result of salinising the root medium, and could reconcile this with the Lockhart description of growth only if P was close to Y and an undetectably small change in P had occurred.

The slower phase of full recovery is difficult to account for. Pritchard et al (1990) found that, following cold treatment, elongation of maize roots recovered only after the production of new cells ; those expanding at time of cold treatment did not resume growth. A partially irreversible effect may have occurred due to osmotic shock, but detailed examination of cell size profiles would be required to resolve this.

Waldron et al (1985) also concluded that the effects of short periods of salinisation of the root medium upon leaf elongation rate in *Beta vulgaris* were a water stress phenomenon, because they were reversible. These authors also reported that, on dark/light and light/dark transition, leaf elongation rates changed dramatically within seconds whilst stomatal responses were over a period of 10 minutes. Both times closely match the observations made here with respect to salinity transitions.

Rice leaf elongation rate was observed to show transients within minutes of light/dark and dark/light transitions (Cutler et al., 1980). They also concluded that the rate of water uptake normally limits the rate of leaf elongation, though the basis of their conclusion, from experiments in which leaf elongation rate was increased by the application of hydrostatic pressure to the roots, is questioned by Cosgrove (1981).

Thiel et al (1988) considered that osmotic effcts on turgor pressure in the expanding zone accounted for effects of root medium salinisation on the LER of barley leaves. Their data contrast markedly with that described here for rice. The initial reduction in LER (at about 10 minutes) was proportional to the external concentration in the 40-120 mM NaCl range (while rice elongation stopped immediately and completely at 50 mM). In barley, partial recovery to new, reduced rates of elongation was gradual over a 1 hr period, whilst in rice it was abrupt following an intervening lag phase proportional to the external concentration. The inference of these data is that growth of rice and barley is very different ; in barley wall extensibility has a more limiting role.

Short Term Effects in Expanded Leaves

When growth in rice is limited by water supply, turgor pressure in the expanded tissue would be greater than in the expanding tissue (Cosgrove, 1981). Thus a change in external water potential that caused elongation to stop might not cause sufficient reduction in leaf turgor to lead the stomata to close. Interestingly, the intercellular concentration of CO_2 decreased with increasing external salt or mannitol

concentration, suggesting that stomatal conductance was affected proportionately more than non-stomatal of aspects of gas exchange. This contrasts with the situation following longer term exposure to salinity, when salt has accumulated in the leaves, where intercellular CO_2 remained constant while stomatal aperture decreased (Yeo et al., 1985) ; suggesting that both stomatal and non-stomatal conductances were reduced by internal salt.

The Causes of Growth Reduction after the Transient Stoppage

There are many possible reasons (which the data do not resolve) why the new growth rate is lower. The rate at which the cell can expand would be limited by the rate at which water moved in and this in turn would be limited by the rate at which osmotic solutes accumulated.

Active solute accumulation competes with wall loosening for protons in the apoplast of the expanding region, which raises the apoplastic pH and so reduces wall extensibility. The hydraulic conductance of the pathway from the external medium to the expanding cells might also be reduced by salt treatment. There is some evidence (for discussion and references see Yeo et al., 1987) that physiological stresses decrease the conductance of root membranes or plasmodesmata. For the same driving force, this would reduce the water supply to the expanding zone.

Munns and Termaat (1986) forcefully conclude that leaf expansion of non-halophytes is not limited by water deficit. The central argument is that root previous elongation rate. It is hard to conceive that anything other than water supply could be perceived, transmitted and translated into a stoppage of growth in the timescale observed. I cannot exclude such possibilities as the transport of messages from root to shoot altering wall extensibility (Termaat et al., 1975 ; Munns and Termaat, 1986). But I do not yet feel that I need invoke an explanation more complicated than the limitation of water supply which has been used to account for the abrupt resumption of elongation growth.

The longer-term (days and weeks) effects of salt are all consistent with damage resulting from excess accumulation of salt in the leaf lamina with the transpiration stream (see Yeo and Flowers 1986, 1989), manifest as premature leaf mortality. Damage to the leaves is amplified by, and may be initialised by, extracellular salt accumulation (Flowers et al 1991). Salt accumulation in the leaves reduces their photosynthetic efficiency before leaves die and this, in association with early senescence, leads to ever-decreasing productivity. Eventually, lack of photosynthate impairs root function which appears to be independent of salinity per se at the concentrations considered here (Yeo and Flowers, 1984). It is as meaningless as it is unnecessary to determine what kills the plant in the end. But the turning point is likely to come when salt transport exceeds new growth, and consequently the maintenance of growth is vital.

Implications for Breeding for Salt Resistance

The separation of osmotic and ion toxicity effects assumes a major practical significance in the breeding of plants with resistance to salinity. In rice, there is ample variation between (Yeo et al., 1990) and within (Yeo et al., 1988) varieties to enable selection of parents with lower rates of NaCl transport. If salt uptake is always detrimental, then selection for salt "exclusion" carries no penalty and would thus be an aim of a breeding programme. If not, then salt exclusion would have a cost and the decision on breeding strategy becomes more complex.

At low (50mM) salinity, all the significant effects on growth and productivity resulted only from long-term exposure. Reduction of NaCl uptake would reduce these effects without limiting the ability of the plant to accommodate to an external salinity of 50 mM. Since this is a concentration which is damaging agriculturally, rice does fall within the category where salt exclusion alone is a viable option (see Yeo and Flowers, 1989). At higher concentrations growth is reduced and, since one of the more probable explanations is an inadequate rate of osmotic adjustment, removing the ability to achieve this in part with NaCl is a path to be followed with caution.

There were minor varietal differences in the response of elongation growth to NaCl, KCl and

mannitol which may, if examined in a meaningfully large number of genotypes, reflect differences in relative transport of Na and K or of their ability to substitute for one another. There were no clear differences in the short-term responses of the tall and dwarf varieties although they are quite extreme in their growth rate and growth form. The growth rate of Pokkali was no more or less sensitive to salt than was that of IR 2153. I am led to conclude that the vigour of the tall varieties is of advantage in the long term only, and this reinforces the earlier suggestion (Yeo and Flowers, 1984) that this is through a dilution effect of the large volume of the vegetative shoot. Although there is a circumstantial correlation between the survival of salinity and the vigour of the tall plant type (Yeo et al 1990), there does not appear to be a disadvantage per se in improved plant types, provided that their reduced stature can be compensated by selection for lower salt transport.

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摘 要

稈長이 다른 水稻 2品種에 대하여 NaCl, KCl, Mannitol을 處理하고 잎의 伸長과 光合成能의 反應을 調査하였다. 그리고 鹽處理에 의하여 잎의 伸長이 일시적으로 停止하고 伸長率이 鈍化되는 현상 및 높은 濃度에서 光合成能이 低下되는 원인에 대하여 考察하였다.

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