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Mangrove Plants and Salts: Salt Tolerance Mechanism of Mangrove

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ABSTRACT

Mangrove plants are distributed along coastal and estuarine areas of the sub-tropical and tropical regions of the world which include Okinawa, Japan. These plants are called halophytes which posses peculiar physiological mechanisms for salt control. The characteristic distribution of mangrove plants is observed as conditioned by tidal regime and salinity.

Absorbed and accumulated inorganic ions as well as other substances participating in osmotic adjustment in leaves and roots were analyzed. Concentrations of Na^+ and Cl^- ions in the leaves of mangrove plants distributed in areas directly affected by sea water were very high. On the other hand, mangrove plant species found upstream or deep in the forest contained low levels of Na^+ and Cl^- ions. In both cases, however, concentrations in leaves were found to increase leaf aging. The leaf thickness also increased with aging and ion concentrations. Comparison of the Na^+ and Cl^- ion concentration in the leaves during the dry and rainy seasons was also made. Leaves in the dry season contained higher levels of both the ions than leaves during the rainy season. This suggests that transpiration from leaves was more vigorous during the dry season and intake of water and salt was enhanced.

Highly absorbed cations were detoxicated by organic acids in the plant. The principal organic acids found in the leaves were malic acid and oxalic acid and the amount of these two acids was higher in old leaves than in immature ones. Many mangrove species adjust osmotic pressure in the cell with organic acids and increased water volume in the cell. Species with salt glands can discharge excessively absorbed salts from the plant body.

INTRODUCTION

Mangrove plants are one of the typical halophytes distributed in river-mouth and seashore areas of sub-tropical and tropical regions of the world. The distribution of mangrove plants has been reported (Barth, 1982). Six species of mangrove plants covering an area of approximately 400 ha have been identified in the Nansei islands, Okinawa, Japan. Characteristic of many mangrove plants is the fact that they can grow very well within wide ranges of salinity which can reach a maximum of approximately 3% NaCl. Notable are those belonging to the Rhizophoraceae which produce viviparous seeds. This seed matures completely on the tree and may germinate in its locality or be distributed to other areas following seawater current movement. The mangrove forest areas of Southeast Asia are decreasing. This reduction is due to many reasons, foremost of which are: production of charcoal for fuel, development of fish and shrimp ponds, logging and ultimately regional development needs for new housing areas. Preservation of the environment and reforestation of mangrove areas as energy sources is going on. Extension of young mangrove trees and methods of tree planting are introduced for reforestation of the destroyed mangrove forests. In this paper we report results of our studies on optimal growth conditions for viviparous seeds of two mangrove species, as well as our investigation on salinity level in cultured solutions for the efficient production of young mangrove trees.

MATERIAL AND METHODS

Mangrove plants and cultivation method

Bruguiera gymnorrhiza L. Lam (Japanese name: Ohirugi) and *Kandelia candel* L. Druce (Japanese name: Mehirugi) were used in the experiment. Viviparous seeds of these two mangrove species were collected from Iriomote-jima island of Okinawa prefecture, Japan. *B. gymnorrhiza* and *K. candel* were cultivated in a 1/2000 Wagner-pot and with air continuously supplied through the bottom of the pot.

Cultivation conditions were as follows: temperature was set at 30°C for daytime and 25°C for nighttime; light and dark condition was 12 h and 12 h with light supplied by 50,000 lux fluorescent lamp; relative humidity was controlled at 50–70% in a plant growth cabinet (Koito Inc.). Standard culture solution used was the designated condition for No. 1 and No. 2 Otsuka liquid fertilizer (Otsuka Chemical Inc.) as shown in Table 1. The other condition was prepared D.W., F-20, F-50, F-80 and F-100 (Table 2). F-20 contains 0.6% NaCl in solution. F-50 contains 1.5% NaCl in solution. F-80 contains 2.4% NaCl in solution. F-100 contains 3.0% NaCl in solution. The culture solution was changed every 2 weeks for 4 months and the ion concentration of the final culture solution was analysed. The internode number, a plant growth indicator, was counted at 2-week intervals for 4 months.

Preparation of sample for analysis

Plants cultured for 4 months were used for the experiment. Leaves, rhizophore and roots of each plant were separated and washed carefully with deionized water (DW), especially the root parts (Fig. 1). Each sample was cut and homogenized for 5 min in a blender with DW. The homogenate was analyzed for inorganic ions and organic acid content.

Inorganic ion analysis

Inorganic ions (cations and anions) of the homogenate were analyzed by ion chromatography (Shimadzu Ion Chromatography IC-6A, Shimadzu Inc.). Conditions were as follows: 5 mM HNO_3 solution as eluent and IC-C1 as column for monovalent cations (Na^+, NH^{4+} and K^+) analysis, (electroconductivity about 2500 $\mu S\ cm^{-1}$); eluent for divalent cations (Mg^{2+} and Ca^{2+}) was 40 mM tartaric acid and 20 mM ethylenediamine solution (electroconductivity about 800 $\mu S\ cm^{-1}$) and IC-C1 was used as column, eluent for anions (F^-, Cl^-, NO_2^-, PO_4^{3-}, Br^-, NO_3^- and SO_4^{2-} was 1 mM *p*-hydroxybenzoic acid and 1.1 mM *N,N*-diethylethanol amine solution (electroconductivity about 120 $\mu S\ cm^{-1}$) and IC-A1 was used as column.

Organic acids analysis

A part of the homogenate was freeze-dried. After butyl esterification, the sample was analyzed for organic acids content by gas chromatography (GC-7AG, Shimadzu Inc.). The gas chromatography was equipped with a flame ion detector (FID) and 2 m × 3 mm (inner diameter) glass column packed with Reoplex 400 on 80–100 mesh Chromosorb AW-DMCS. The column temperature was held at 40°C for 1 min., then programmed at 5°C/min up to 210°C.

TABLE 1

Ion components and concentrations in standard culture solution

Ion	Concentration (ppm)
Na	0
NH_4	33
K	210
Mg	50
Ca	170
Cl	10
PO_4	45
NO_3	640
SO_4	210

TABLE 2

NaCl concentration in culture solution

Condition	Fertilizer*	NaCl%	NaCl ratio
D.W.**	–	0	0
F-O	+	0	0
F-20	+	0.6	x 1.0
F-50	+	1.5	x 2.5
F-80	+	2.4	x 4.0
F-100	+	3.0	x 5.0

*Ohtsuka liquid fertilizer No.1 + No.2 (1:1).
**De-ionized water.

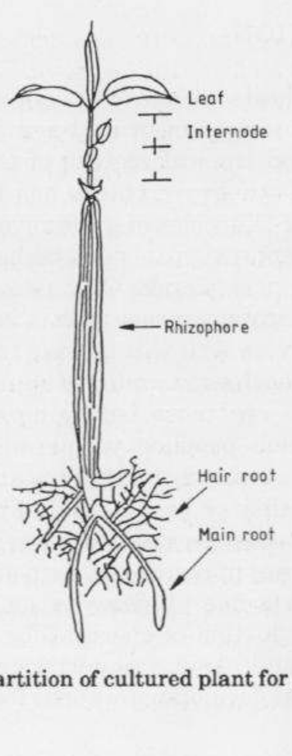

Fig. 1. Partition of cultured plant for analysis.

TABLE 3

Internode number of 10 *Kandelia candel* seedlings under various culture conditions

Month	Condition					
	D.W.	F-0	F-20	F-50	F-80	F-100
0.5	0	0	0	0	0	0
1	0	10	10	10	1	0
2	4	17	23	20	9	4
4	6	48	51	42	33	9

TABLE 4

Internode number of 10 *Bruguiera gymnorrhiza* seedlings under various culture conditions

Month	Condition					
	D.W.	F-0	F-20	F-50	F-80	F-100
0.5	0	0	0	0	0	0
2	13	32	32	30	28	24
4	34	60	76	50	40	39

RESULTS

Cultivation of *Bruguiera gymnorrhiza* and *Kandelia candel* under several culture conditions

The internode number was counted at 2-week intervals for 4 months until harvest. Internode numbers of *Kandelia candel* and *Bruguiera gymnorrhiza* are shown in Tables 3 and 4. These results are the true total internode number of 10 viviparous seeds. *K. candel* internode number under DW condition was an average of 0.6, while, *B. gymnorrhiza* was 3.4. *K. candel* grown under F-20 conditions produced 5.1 internodes, while *B. gymnorrhiza* produced 7.6 internodes. The internode number gradually decreased with an increase in NaCl concentration in the culture solution. *K. candel* internode number under F-100 condition dropped to an average 0.9 and new leaves did not develop. It was observed that root development under DW condition was poor, and only the main root developed without absorptional fine root hairs. *B. gymnorrhiza* grown under F-100 conditions produced 3.9 internodes. Growth rate of the stretching parts was inferior and each leaf area was small. The main root developed under DW condition and absorptional fine root could hardly be recognized; the leaves were also small. In sharp contrast, plants grown under F-20 conditions produced many internodes with development of many main and hair roots; also, the leaf area was wide. Roots of plants grown under F-100 conditions were mostly main root; also, some buds of viviparous seeds withered after new leaf development. On the other hand, plants grown under F-20 conditions developed many main roots and fine roots (hair roots). The leaves were big and dark green, while some plants developed some branches. Main root of F-100 condition was more recognizable than root of DW condition, and development of fine root was inferior to F-20 condition. Internode number and leaf areas gradually decreased with increased NaCl concentration in the culture solution. However, leaf thickness gradually increased.

Ion components and their concentrations in the final culture solution are shown in Table 5. After culturing plants for 4 months, the ion components of the culture solution show a similar trend for both *B. gymnorrhiza* and *K. candel*. Na^+, K^+, Ca^{2+}, Cl^- and SO_4^{2-} ions were detected in DW. These results suggest that these ions passed through the root and viviparous seed tissues into the DW. Concentrations of K^+, NO_3^- and PO_4^{3-} — essential elements for plant growth — typically decreased under F-20 conditions. The same trend was observed under F-50 conditions. Decrease ratio of each ion in the solution gradually decreased with increased NaCl concentration in the culture solution.

Inorganic ion concentration in harvested plants

Ion analysis results for *Kandelia candel* are shown in Figs. 2 to 4. The main cation, most widely distributed in the plant tissues was Na^+, followed by K^+, Mg^{2+} and Ca^{2+} cations. The main anion found in the tissues was Cl^-. But, SO_4^{2-} was also detected in very low concentrations in the tissues. SO_4^{2-} is not shown in the Table.

Na^+ concentration in the leaf increased with a corresponding increase in NaCl concentration in the culture solution. The highest concentration of K^+ was determined under F-20 condition (12.30 meq) and secondly under F-0 condition (10.90 meq). The ratio of Na/K in the leaf gradually increased with a corresponding increase in NaCl concentration in the culture solution. F-80 condition gave the highest ratio of 3.63. F-20 condition indicated the best plant growth. Mg^{2+} and Ca^{2+} reached a maximum of 1.65 meq and 1.24 meq, respectively. Distributed main anion was Cl^- and its concentration increased with a corresponding increase in NaCl concentration in culture solution. Cl^- concentration was found highest at 30.46 meq under F-80 conditions. Na^+ concentration

TABLE 5

Ion concentrations (ppm) in culture solutions taken in the last 2 weeks of 4 months culture period of *Kandelia candel* (unit: ppm)

Ion	Condition											
	D.W.		F-0		F-20		F-50		F-80		F-100	
	B*	U**	B	U	B	U	B	U	B	U	B	U
Na	0	2	0	8	2400	1580	5400	4600	9440	6810	11,800	9920
NH_4	0	0	33	5	33	6	33	0	33	0	33	0
K	0	1	210	160	210	120	210	150	210	158	210	205
Mg	0	0	50	32	50	23	50	19	50	28	50	27
Ca	0	4	170	130	170	125	170	156	170	155	170	160
Cl	0	2	10	11	3650	1650	9110	7046	14,570	12,370	18,300	16,700
PO_4	0	0	45	20	45	0	45	0	45	0	45	0
NO_3	0	0	640	530	640	430	640	460	640	600	640	610
SO_4	0	1	210	171	210	160	210	105	210	230	210	220

*Standard solution.
**2 weeks culture solution.

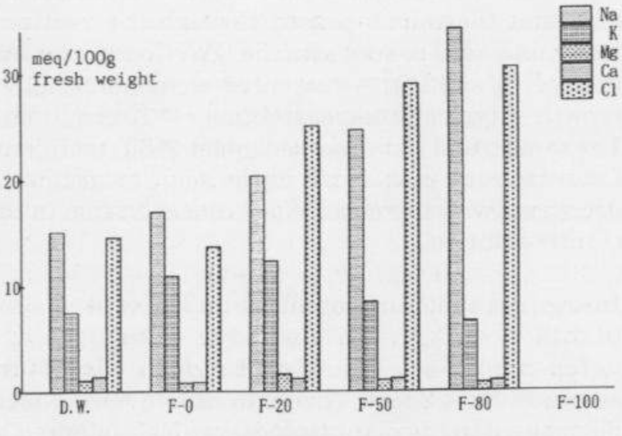

Fig. 2. Ion concentration in *Kandelia candel* leaf.

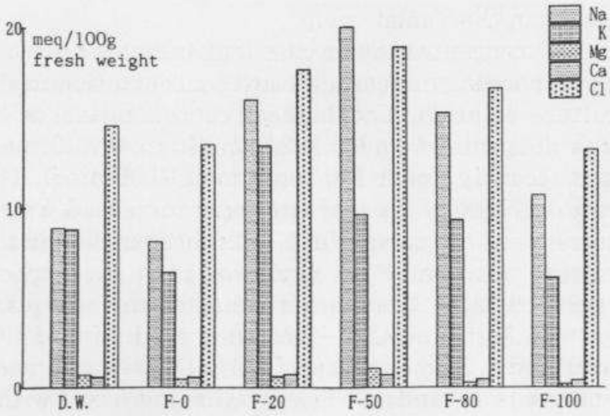

Fig. 3. Ion concentration in *Kandelia candel* rhizophore.

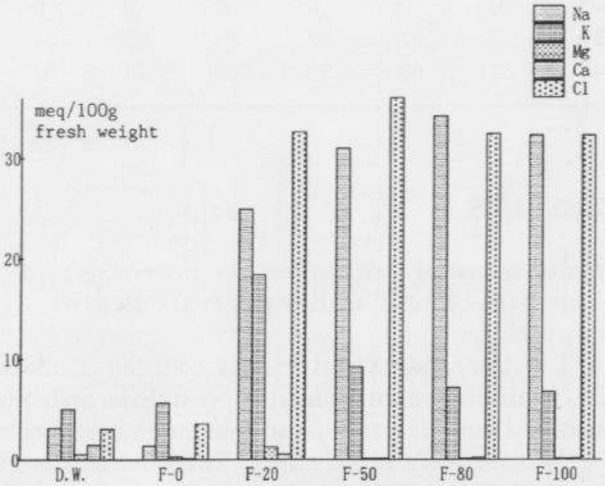

Fig. 4. Ion concentration in *Kandelia candel* root.

in the rhizophore was found to reach the highest level of 20.00 meq under F-50 conditions. On the other hand, the highest level of K^+ was found to be 13.45 meq under F-20 conditions. Mg^{2+} and Ca^{2+} levels in the rhizophore were found to be lower than those in the leaf. Also, distributed main anion in the rhizophore was Cl^- and the highest amount 18.50 meq was detected under F-50 conditions.

Na^+ concentration in the root was found to be lowest (1.40 meq) under F-0 conditions. The highest level (34.10 meq), was found under F-80 conditions. K^+ concentration in the root reached highest level of 18.40 meq under F-20 conditions which gave the best

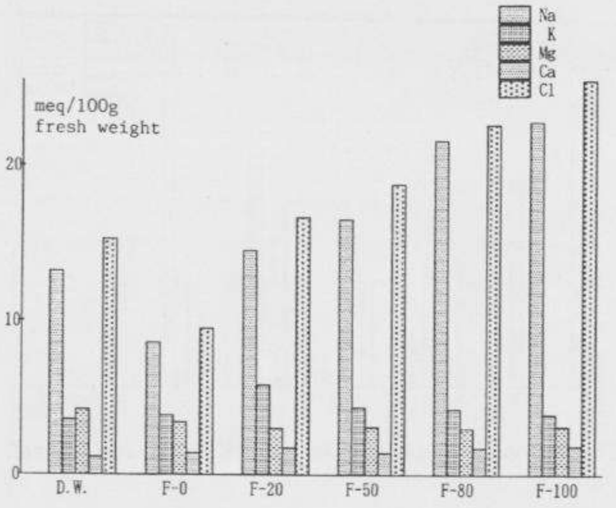

Fig. 5. Ion concentration in *Bruguiera gymnorrhiza* leaf.

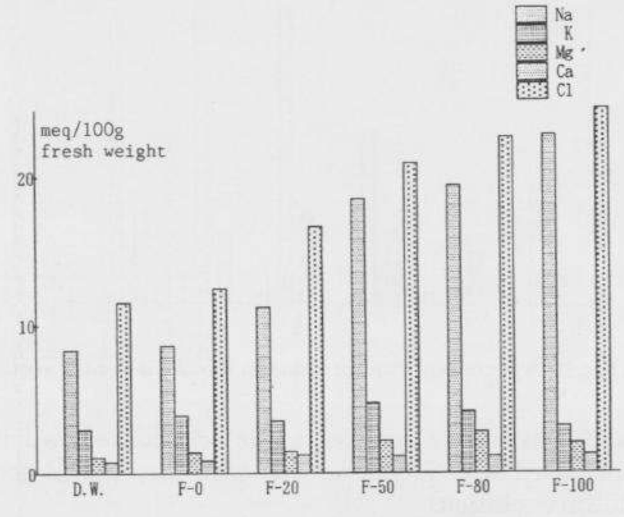

Fig. 6. Ion concentration in *Bruguiera gymnorrhiza* rhizophore.

growth among the conditions tested. Na/K ratio of DW condition was 0.64, F-0 condition was 0.25. But, Na/K ratio number increased according to NaCl concentration in the culture solution. Then, Na/K ratio of F-100 condition was 4.79. Main anion in the root was Cl^- and its concentration from F-20 to F-100 conditions was over 30 meq.

Results of ion analysis for the *Bruguiera gymnorrhiza* plant are shown in Figs. 5–7. The main cation distributed in the tissue was Na^+, while K^+, Mg^{2+} and Ca^{2+} cations followed closely. The main anion distributed in the tissues was Cl^-. However, SO_4^{2-} was also detected in very low concentration levels in the tissues. SO_4^{2-} is not shown in the tables. Na^+ concentration in the leaf was recognized according to the increase in NaCl concentration in the

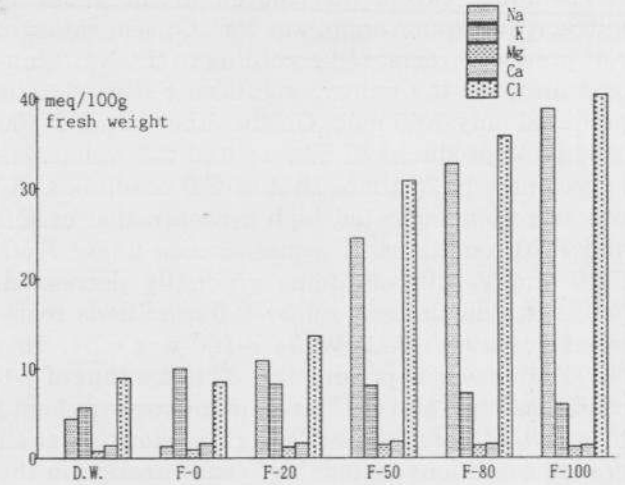

Fig. 7. Ion concentration in *Bruguiera gymnorrhiza* root.

culture solution. Na^+ concentration in the leaf under F-100 conditions was 22.80 meq and this was the highest level attained among the culture conditions. K^+ concentration, essential for growth, in the leaf under F-20 conditions was 5.80 meq and was higher than in other conditions. Ratio of Na/K in the leaf, F-0 condition indicated the lowest 2.23 and F-100 condition was 5.83. Na/K ratio in *B. gymnorrhiza* leaf was higher than that of *K. candel*. Concentration of distributed Mg^{2+} in the leaf was within 3.00 meq to 4.20 meq. And Ca^{2+} concentration was within 1.15 meq to 1.86 meq. Both divalent cation concentration in the leaf of *B. gymnorrhiza* were higher than that found in *K. candel* leaf. The main anion distributed in the leaf was Cl^- and SO_4^{2-} was also detected. This SO_4^{2-} concentration increased slightly according to NaCl concentration in the culture solution. Cl^- concentration under F-20 conditions was 9.50 meq as the lowest and F-100 condition produced the highest concentration (25.50 meq).

The main cation distributed in the rhizophore was Na^+ and its concentration gradually increased according to NaCl concentration in the culture solution. F-100 condition indicated 22.67 meq. K^+ concentration in the rhizophore under F-50 conditions was 4.72 meq. K^+ concentration under F-20 conditions was 3.58 meq. Na/K ratio in the rhizophore under DW conditions was 2.78 and the other conditions gradually increased with NaCl concentration in the culture solution. Na/K ratio under F-100 conditions was 7.08. Mg^{2+} and Ca^{2+} cations in the rhizophore was found to be lower than in the leaf under all growth conditions tested. The main anion distributed in the rhizophore was Cl^- and SO_4^{2-} was also detected.

The main cation distributed in the roots as nutrient absorption organ was Na^+. Concentration of Na^+ gradually increased according to the NaCl concentration in the culture solution. F-0 conditions produced only 1.65 meq. On the other hand, F-100 conditions produced 37.89 meq and this value was approximately 23 times that of F-0 conditions. K^+ concentration indicated high concentration at F-0 and F-20 conditions. K^+ concentration under F-50, F-80 and F-100 conditions gradually decreased. Na/K ratio in the root under F-0 conditions registered the lowest 0.17, while F-100 was 6.34. This Na/K value was approximately 37 times that of F-0 condition. Mg^{2+} and Ca^{2+} levels in the root was found to be lower than in the leaf and rhizophore under all growth conditions tested. Mg^+ concentration in the root was lower than Ca+ concentration. The main anion distributed in the root was Cl^- and SO_4^{2-} was also detected. Cl^- concentration under F-100 conditions was the highest 40.31 meq.

Organic acid content in cultured plants

Many halophytes regulate osmosis in the plant body to maintain normal physical mechanisms. Regulation under conditions of excess absorbed cations may be obtained through the use of organic acids and other organic substances (Luttge and Smith, 1984). In this study, organic acids (diacids and triacids) which are osmosis control substances in the plants were analysed.

Results of analysis of *Kandelia candel* leaves and roots are shown in Figs. 8 and 9. Previous studies on *K. candel* and *Bruguiera gymnorrhiza* leaves and roots have been reported from natural mangrove forests (Kato et al., 1986a,b). The main organic acids in the plants were found to be oxalic acid and malic acid. The best growth condition of F-20 showed lower organic acid content in the leaves and roots than those found under other culture conditions (F-50 and F-80 conditions). Malic acid in the leaf reached a highest concentration of 15.56 meq under F-80 conditions. Oxalic acid and malic acid in the roots were present at concentrations higher than the other organic acids. Especially, malic acid concentration increased according to NaCl concentration in culture solution. The highest value, 22.38 meq, was obtained under F-80 conditions. Analysis results of *B. gymnorrhiza* leaves and roots are shown in Figs. 10 and 11. F-20 condition produced the best growth and the concentration of oxalic acid also was the highest concentration than other growth conditions. Oxalic acid and malic acid concentration in the leaf were found to be higher than the other organic acids. Oxalic acid and malic acid in the root were present at concentrations higher than the other organic

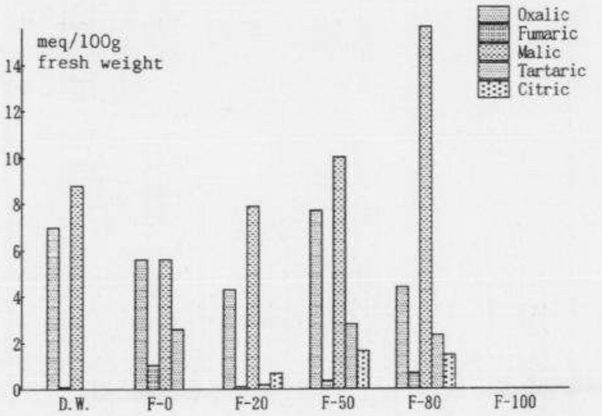

Fig. 8. Organic acid concentration in *Kandelia candel* leaf.

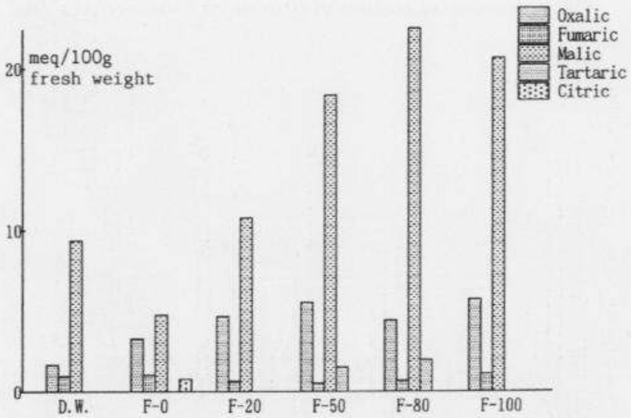

Fig. 9. Organic acid concentration in *Kandelia candel* root.

acids. As with *K. candel*, malic acid concentration increased with increased salt concentration in the culture solution.

DISCUSSION

Relationship of NaCl concentration and growth of *Kandelia candel* and *Bruguiera gymnorrhiza*

Results of our study on the growth of *Kandelia candel* and *Bruguiera gymnorrhiza* for 4 months under several culture conditions showed F-20 conditions produced the best plant growth. The NaCl concentration at this level (F-20) is 0.6%. Streams in natural mangrove forest areas usually bring in fresh water from upper river areas (mountains). Salt concentration of these mangrove areas is very changeable with the inflow of fresh water and regular tide of sea water. Salt concentration ranges from 0% up to seawater NaCl concentration level. These mangrove forest areas are regularly affected by the daily sea tide. Salt concentrations were fixed in this study.

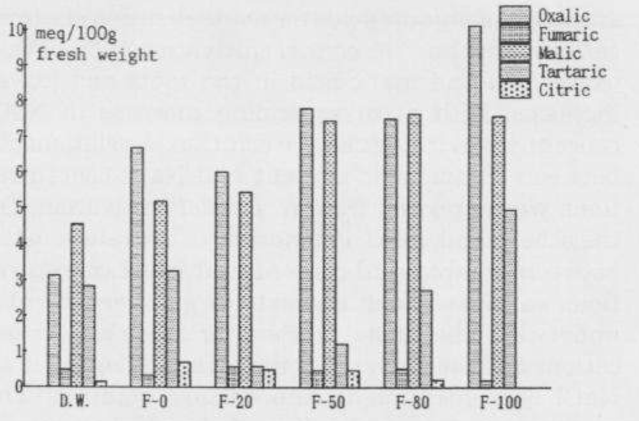

Fig. 10. Organic acid concentration in *Bruguiera gymnorrhiza* leaf.

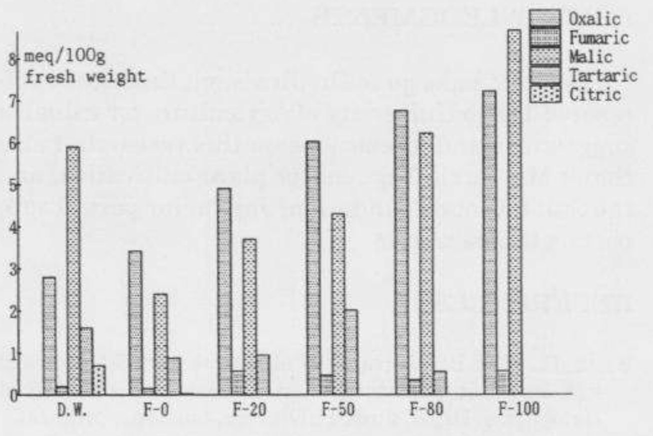

Fig. 11. Organic acid concentration in *Bruguiera gymnorrhiza* root.

The distribution area of *K. candel* and *B. gymnorrhiza* is from middle to upper areas which are affected by seawater through river to mangrove forest, perhaps F-20 condition as the best growth culture was similar to water component condition of these two kinds of mangrove plants area. Essential elements for plant growth such as K^+, NH_4^+, NO_3^- and PO_4^{3-} correspond to K, N and P. After the culture period, ion components decreased in the F-20 condition which is the best growth culture condition. As its components were gradually decreasing, it was observed that the NaCl concentration was increasing in the culture solution. These results suggest that absorbed essential elements, possibly NaCl, suppressed other cations and anions which were essential for growth of *K. candel* and *B. gymnorrhiza*. The ratio of Na^+ and Cl^- concentrations were typically decreased compared with other ions. These two mangrove species might preferentially absorb K^+ for normal growth. Distribution of *K. candel* and *B. gymnorrhiza* in the natural mangrove forests is not directly affected by tidal seawater and they are not found in fringe areas of mangrove forests. Also, thick growth areas of these two mangrove species are found in the inner areas of mangrove forest and the upper stream area. The experimental F-20 condition (0.6% NaCl) of this study may be similar to NaCl and other ion components in natural conditions. If level control (high and low) of culture solution corresponded to tidal seawater, further optimum growth and the best NaCl concentration for *K. candel* and *B. gymnorrhiza* growth will be confirmed.

Inorganic ion components in harvested *Kandelia candel* and *Bruguiera gymnorrhiza* plants

The physiological mechanism of halophytes is studied under several conditions. In general, halophytes adjust to high salt conditions as follows: (1) control of Na^+ inflow at root cell; (2) once entered, excess salts are discharged from root cells; (3) absorbed and translocated excess accumulation salts, retranslocate to root through sieve tube and discharge from root; (4) absorbed excess salts accumulate in roots and stems for regulation of salt accumulation into the leaf; (5) translocated excess salts until full storage in salt hair of differentiation of epidermal cell of leaf and excreted from the plant body by disruption of hair root; (6) excess salts excreted from salt glands of leaf surface; (7) excess salts storage in vacuole cell of mesophyll cell and increase cell water for osmosis adjustment; (8) excess cations are neutralized by organic acids and some amino acids. Halophytes respond with a combination of these methods for osmosis control.

K. candel and *B. gymnorrhiza* are distributed in the upper areas of the natural mangrove forest at Okinawa and tropical countries in the world. The main distributed cation in the leaf was Na^+ which entered root cell through membrane and translocated into leaf of *K. candel* and *B. gymnorrhiza*. Na^+ concentration in *K. candel* leaf was higher than *B. gymnorrhiza* leaf. The Na^+ concentration was 1.40 times in F-20, 1.49 times in F-50 and 1.57 times in F-80 conditions. These results show the different growth conditions of mangrove plants that is reflected by the difference in distribution area of the mangrove species in the natural ecosystem. Accordingly, salinity in *B. gymnorrhiza* distribution areas is higher than in *K. candel* distribution areas. *B. gymnorrhiza* root is able to control as much ion absorption as possible. In the case of *K. candel*, ions may easily be transported to the leaf through the stem and accumulate in the leaf. Usually, K^+ was absorbed under high salt condition. The cation K^+ is important for biosynthesis of starch, opening and closing of stomata, oxidative phosphorylation, metabolism of protein, related to pH control and osmosis adjustment in the cell. However, the physiological action of Na^+ in the plant is not well understood at present. Mangrove plants are classified in the C_3 plant group and plants in this group need twice as much water as C_4 plants for normal growth. Mangrove plants can absorb nutrients in water from low nutrient conditions of their growth environment, and transport these to the leaf while water is transpired to the air. The absorbed nutrients remain in the leaf and their concentration gradually increases. Part of the rhizophore is a route for absorbed ions and water into the leaf. *K. candel* distributed low amounts of each ions. On the other hand, for *B. gymnorrhiza* a tendency was observed in this rhizophore part to accumulate these ions. These results indicate that rhizophore may be useful as a preserving mechanism for excess ions for normal physiological processes of the plant.

The total cations in *B. gymnorrhiza* roots was higher than in the leaf. This result shows that at first, absorbed ions accumulate in the root and then necessary amounts of each ion are transported through the rhizophore to the leaf for normal physiological plant processes. This process in *B. gymnorrhiza* is more advanced than in *K. candel*, but *K. candel* may also have the same mechanism for absorption of nutrients. After ion transport into the leaf, the translocation of ions from leaf to the root and ion accumulation in the root needs to be studied further.

The Cl^- ion is the pair anion of absorbed cations. Physiological actions of this absorbed Cl^- are important for oxygen generation of the photosynthetic process, and participation to dehiscent water with Mn of micronutrients (Izawa et al., 1969; Critchely, 1985). Absorbed inorganic ions (NO_3^-, PO_4^{3-}, SO_4^{2-}) are utilized for plant composition. These absorbed inorganic ions, however, cannot respond to pH changes, control of osmotic pressure and control of turgor pressure in the cell and there is no equivalent molar ratio against absorbed cations. When halophytes grow under high salinity conditions, they stimulate synthesis of organic acids for neutralization of excess cations. Results of *K. candel* cultivation showed that oxalic acid and malic acid in the roots and leaves increased with a corresponding increase in NaCl concentration in the culture solution. A relationship between organic acid content and NaCl concentrations was supposed from *K. candel* cultivation. On the other hand, for *B. gymnorrhiza*, the relationship between organic acid content and NaCl concentrations was not so clear. However, *B. gymnorrhiza* also underwent the same process for absorbed excess cations and the amount of organic acids depended on NaCl concentration in the culture solution. The mechanism of neutralization of absorbed excess cations with organic acids for two mangrove plants is recognized.

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