PHYTOHORMONE DIRECTED TRANSPORT OF IONS IN RICE (*Oryza sativa* L.) SEEDLINGS

by
SHAHANA AHMED
B.Sc. Hons. (Dhaka), M.Sc. (Dhaka)

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J. L. Karmoker

Dr. Jadu Lal Karmoker
Professor
Department of Botany
University of Dhaka

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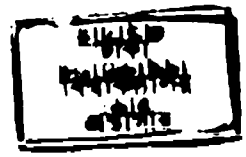

Dedicated to my parents

who inspired me

all the time

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SUMMARY

Abscisic acid (ABA) inhibited the accumulation of monovalent cations like K^+ and Na^+ in excised root systems of rice seedlings. ABA also inhibited the accumulation of divalent cations like Ca^{2+}, Mg^{2+} and Fe^{2+} in excised root systems.

In intact seedlings, ABA inhibited K^+ and Na^+ accumulation both in the root and the shoot.

ABA (10^{-5} M) stimulated Ca^{2+} accumulation in the root and the shoot of intact seedlings but at lower concentration, ABA (10^{-7} M) decreased the accumulation of Ca^{2+} in the shoot of intact rice seedlings.

ABA increased Mg^{2+} accumulation in the root but decreased that in the shoot of intact rice seedlings.

The accumulation of Fe^{2+} was decreased by ABA in the root of intact seedlings. ABA also decreased Fe^{2+} accumulation in the shoot after an initial promotion.

ABA increased Cl^- accumulation in the root and the shoot of intact rice seedlings.

The accumulation of NO_3^- in the root was increased whereas it was decreased in the shoot of intact seedlings.

ABA decreased phosphate accumulation both in the root and in the shoot of intact rice seedlings.

ABA inhibited net influx and long distance transport of K^+ and Na^+ from the root to the shoot of intact rice seedlings. On the other hand, ABA increased net influx and long distance transport of Ca^{2+}. At lower concentration, ABA (10^{-7} M) stimulated net influx and long distance transport of Mg^{2+} after an initial inhibition while at higher concentration (10^{-5} M), ABA decreased that in rice seedlings.

The net influx of Fe^{2+} was inhibited in intact seedlings. Long distance transport of Fe^{2+} was also inhibited by ABA after an initial promotion. On the other hand, ABA caused a stimulation in net influx and long distance transport of Cl^- after an initial inhibition. ABA inhibited net influx and long distance transport of NO_3^- and phosphate from the root to the shoot.

In excised root systems, kinetin inhibited the accumulation of K^+ and Na^+. However, kinetin (10^{-6} and 10^{-5} M) increased Ca^{2+} accumulation. At lower concentration of kinetin (10^{-7} and 10^{-6} M) increased the accumulation of Mg^{2+}. Kinetin increased Fe^{2+} accumulation after an initial decrease in excised root systems of rice seedlings.

In intact seedlings, kinetin decreased the accumulation of K^+ in the root after an initial promotion but had no significant effect on K^+ accumulation in the shoot except at 10^{-5} M. At 10^{-5} M kinetin increased K^+ accumulation.

Kinetin caused an increase in Na^+ accumulation in the root but it was decreased in the shoot of intact seedlings.

In intact rice seedlings, Ca^{2+} accumulation was increased in the root but decreased that in the shoot by kinetin.

Kinetin stimulated the accumulation of Mg^{2+} in the root of intact seedlings after an initial inhibition but kinetin decreased that in the shoot of intact rice seedlings.

The accumulation of Fe^{2+} was increased by kinetin in the root and the shoot of intact seedlings.

Kinetin caused a decrease in Cl^- accumulation in the root but increased that in the shoot of intact seedlings.

The accumulation of NO_3^- was inhibited by kinetin in the root and the shoot of intact rice seedlings.

In intact rice seedlings, kinetin increased the accumulation of phosphate in the root and the shoot.

Kinetin decreased both net influx and long distance transport of K^+ and Na^+ in rice seedlings.

Kinetin increased the net influx and long distance transport of Mg^{2+} after an initial decrease. But it inhibited the net influx and long distance transport of Ca^{2+} in intact seedlings. Kinetin at lower concentration (10^{-7} and 10^{-6} M) increased net influx and long distance transport of Fe^{2+} while it decreased that at higher concentration (10^{-5} M).

ABA decreased the root and the shoot growth of intact rice seedlings. On the contrary, kinetin increased the root and the

shoot growth of intact rice seedlings. A relationship between the phytohormone-induced growth and ion transport is discussed.

ABA increased the reducing sugar and total sugar content in the root and the shoot of intact rice seedlings. A correlation between the phytohormone directed sugar level and ion transport is discussed.

ABA decreased H^+ extrusion with a simultaneous inhibition of k^+ accumulation from root of intact rice seedlings. A relationship between H^+ extrusion and K^+ transport is discussed.

CONTENTS

		Page
Summary	...	iii
List of figures	...	xiv
List of tables	...	xix
List of plates	...	xxi
List of abbreviations	...	xxii
Chapter 1 : General Introduction	...	1
1.1. Effects of phytohormones on proton pump	...	5
1.2. Effects of phytohormones on ion transport in excised plant tissue	...	7
1.2.1. Effects of auxins on ion transport in excised tissue	...	8
1.2.2. Effects of gibberellic acid on ion transport in excised tissue	...	10
1.2.3. Effects of abscisic acid on ion transport in excised tissue	...	12
1.2.4. Effects of kinetin on ion transport in excised tissue	...	17
1.3. Effects of phytohormones on ion transport in intact plants	...	19
1.3.1. Effects of auxins in ion transport in intact plants	...	19
1.3.2. Effects of gibberellic acid on ion transport in intact plants	...	20
1.3.3. Effects of abscisic acid on ion transport in intact plants	...	22
1.3.4. Effects of kinetin on ion transport in intact plants	...	24

Chapter 2 : Materials and Methods ... 27

2.1. Plant materials ... 27

2.2. Solution culture technique ... 27

2.3. Preparation of stock solution ... 28

2.3.1. Stock solution of micronutrients ... 28

2.3.2. Stock solution of macronutrients ... 28

2.3.3. Preparation of full strength Hoagland solution ... 29

2.3.4. Stock solution of ABA ... 30

2.3.5. Stock solution of kinetin ... 30

2.4. Culture of plants ... 30

2.4.1. Surface sterilization of seeds ... 30

2.4.2. Growing of plants in solution culture ... 31

2.5. Ion transport experiment with excised root systems ... 33

2.6. Ion transport experiment with intact plants ... 33

2.7. Collection and drying of samples ... 33

2.8. Methods of extraction and measurement od ions in plant tissue ... 35

2.8.1. Extraction of K^+, Na^+, Ca^{2+}, Mg^{2+}, Fe^{2+} and phosphate ... 35

2.8.2. Extraction of chloride and nitrate ... 35

2.8.3. Measurement of K^+ and Na^+ ... 36

2.8.4. Measurement of Ca^{2+}, Mg^{2+} and Fe^{2+} ... 36

2.8.5. Measurement of Cl^- ... 42

2.8.6. Measurement of nitrate ... 42

2.8.6.1. Preparation of 5% salicylic acid ... 42

2.8.6.2. Preparation of 2N NaOH solution ... 44

2.8.6.3. Determination of nitrate ... 44

2.8.7. Measurement of phosphate ... 45

2.8.7.1. Preparation of solution A ... 45

2.8.7.2. Preparation of solution B ... 45

2.8.7.3. Preparation of solution C ... 47

2.8.7.4. Determination of phosphate ... 47

2.9. Methods of extraction and measurement of sugar in plant tissue ... 47

2.9.1. Extraction of sugar ... 47

2.9.2. Measurement of reducing sugar ... 49

2.9.2.1. Preparation of solution I ... 49

2.9.2.2. Preparation of solution II ... 49

2.9.2.3. Preparation of solution III ... 50

2.9.2.4. Preparation of arsenomolybdate 50

2.9.2.5. Preparation of standard glucose solution ... 50

2.9.2.6. Determination of reducing sugar ... 50

2.9.3. Measurement of total sugar ... 51

Chapter 3 : The effect of phytohormones on monovalent and divalent cations transport in excised root systems of rice seedlings ... 55

3.1. Introduction ... 55

3.2. Materials and methods ... 57

3.2.1. Culture of plants ... 57

3.2.2. Methods of ion transport experiment with excised root systems ... 57

3.2.3. Collection and drying of samples ... 57

3.2.4. Methods of extraction of ions ... 58

3.2.5. Measurement of monovalent and divalent cations in excised root systems ... 58

3.3. Results ... 58

3.3.1. The effect of ABA on the accumulation of monovalent cations in excised root systems of rice seedlings ... 58

3.3.2. The effect of ABA on the accumulation of divalent cations in excised root systems of rice seedlings ... 60

3.3.3. The effect of kinetin on the accumulation of monovalent cations in excised root systems of rice seedlings ... 64

3.3.4. The effect of kinetin on the accumulation of divalent cations in excised root systems of rice seedlings ... 64

3.4. Discussion ... 71

Chapter 4 : The effect of phytohormones on monovalent and divalent cations transport in intact rice seedlings ... 74

4.1. Introduction ... 74

4.2. Materials and methods ... 75

4.2.1. Culture of plants ... 75

4.2.2. Methodd of ion transport experiment with intact plants ... 75

4.2.3. Collection and drying of samples ... 76

4.2.4. Method of extraction of ions ... 76

4.2.5. Measurement of monovalent and divalent cations in intact root systems ... 76

4.3. Results ... 76

4.3.1. The effect of ABA on the accumulation of monovalent cations in intact rice seedlings ... 76

4.3.2. The effect of ABA on the accumulation of divalent cations in intact rice seedlings ... 82

4.3.3. The effect of ABA on net influx and long distance transport of monovalent cations in intact rice seedlings ... 90

4.3.4. The effect of ABA on net influx and long distance transport of divalent cations in intact rice seedlings ... 94

4.3.5. The effect of kinetin on the accumulation of monovalent cations in intact rice seedlings ... 99

4.3.6. The effect of kinetin on the accumulation of divalent cations in intact rice seedlings ... 105

4.3.7. The effect of kinetin on net influx and long distance transport of monovalent cations in intact rice seedlings ... 111

4.3.8. The effect of kinetin on net influx and long distance transport of divalent cations in intact rice seedlings ... 117

4.4. Discussion ... 123

Chapter 5 : The effect of phytohormones on anions transport in intact rice seedlings ... 129

5.1. Introduction ... 129

5.2. Materials and methods ... 130

5.2.1. Culture of plants ... 130

5.2.2. Methods of ion transport experiment with intact seedlings ... 130

5.2.3. Collection and drying of sample ... 130

5.2.4. Methods of extraction of anions ... 131

5.2.5. Measurement of anions in intact plants ... 131

5.3. Results ... 131

5.3.1. The effect of ABA on the accumulation of anions in intact rice seedlings ... 131

5.3.2. The effect of ABA on net influx and long distance transport of anions in intact rice seedlings ... 140

5.3.3. The effect of kinetin on the accumulation of anions in intact rice seedlings ... 145

5.3.4. The effect of kinetin on net influx and long distance transport of anions in intact rice seedlings ... 151

5.3.5. The effect of ABA on the growth of intact rice seedlings ... 159

5.3.6. The effect of kinetin on the growth of intact rice seedlings ... 161

5.4. Discussion ... 165

Chapter 6 : Mechanistic aspects of hormonal regulation of ion transport ... 171

Section 6a : The effect of abscisic acid on sugar level and its correlation with transport of ions in intact rice seedlings ... 171

6a.1. Introduction ... 171

6a.2. Materials and methods ... 172

6a.2.1. Culture of plants ... 172

6a.2.2. Methods of ion transport experiment with intact seedlings ... 172

6a.2.3. Collection of sample ... 173

6a.2.4. Method of the extraction of sugar ... 173

6a.2.5. Measurement of sugar in intact plants... 173

6a.3. Results and discussion ... 173

Section 6b : The effect of abscisic acid on H^+ efflux from roots and its correlation with transport of ion in intact rice seedlings ... 181

6b.1. Introduction ... 181

6b.2. Materials and methods ... 182

6b.2.1. Culture of plants ... 182

6b.2.2. Methods of ion transport experiment with intact seedlings ... 182

6b.2.3. Measurement of H^+ accumulation ... 182

6b.3. Results and discussion ... 184

Chapter 7 : Conclusion ... 185

References ... 189

LIST OF FIGURES

			Page
Figure	1	Standard curve for potassium ...	37
	2	Standard curve for sodium ...	38
	3	Standard curve for calcium ...	39
	4	Standard curve for magnesium ...	40
	5	Standard curve for iron ...	41
	6	Standard curve for chloride ...	43
	7	Standard curve for nitrate ...	46
	8	Standard curve for phosphate ...	48
	9	Standard curve for reducing sugar ...	52
	10	Standard curve for total sugar ...	53
	11	The effect of different concentrations of ABA on K^+ accumulation in excised root systems of rice seedlings ...	59
	12	The effect of different concentrations of ABA on Na^+ accumulation in excised root systems of rice seedlings ...	61
	13	The effect of different concentrations of ABA on Ca^{2+} accumulation in excised root systems of rice seedlings ...	62
	14	The effect of different concentrations of ABA on Mg^{2+} accumulation in excised root systems of rice seedlings ...	63
	15	The effect of different concentrations of ABA on Fe^{2+} accumulation in excised root systems of rice seedlings ...	65
	16	The effect of different concentrations of kinetin on K^+ accumulation in excised root systems of rice seedlings ...	66

Figure	17	The effect of different concentrations of kinetin on Na^+ accumulation in excised root systems of rice seedlings ...	67
	18	The effect of different concentrations of kinetin on Ca^+ accumulation in excised root systems of rice seedlings ...	68
	19	The effect of different concentrations of kinetin on Mg^{2+} accumulation in excised root systems of rice seedlings ...	69
	20	The effect of different concentrations of kinetin on Fe^{2+} accumulation in excised root systems of rice seedlings ...	70
	21a	The effect of different concentrations of ABA on K^+ accumulation in the root of intact rice seedlings ...	77
	21b	The effect of different concentrations of ABA on K^+ accumulation in the shoot of intact rice seedlings ...	79
	21a	The effect of different concentrations of ABA on Na^+ accumulation in the root of intact rice seedlings ...	80
	22b	The effect of different concentrations of ABA on Na^+ accumulation in the shoot of intact rice seedlings ...	81
	23a	The effect of different concentrations of ABA on Ca^{2+} accumulation in the root of intact rice seedlings ...	83
	23b	The effect of different concentrations of ABA on Ca^{2+} accumulation in the shoot of intact rice seedlings ...	84
	24a	The effect of different concentrations of ABA on Mg^{2+} accumulation in the root of intact rice seedlings ...	85
	24b	The effect of different concentrations of ABA on Mg^{2+} accumulation in the shoot of intact rice seedlings ...	87
	25a	The effect of different concentrations of ABA on Fe^{2+} accumulation in the root of intact rice seedlings ...	88

Figure	25b	The effect of different concentrations of ABA on Fe^{2+} accumulation in the shoot of intact rice seedlings	...	89
	26a	The effect of different concentrations of kinetin on K^{+} accumulation in the root of intact rice seedlings	...	100
	26b	The effect of different concentrations of kinetin on K^{+} accumulation in the shoot of intact rice seedlings	...	102
	27a	The effect of different concentrations of kinetin on Na^{+} accumulation in the root of intact rice seedlings	...	103
	27b	The effect of different concentrations of kinetin on Na^{+} accumulation in the shoot of intact rice seedlings	...	104
	28a	The effect of different concentrations of kinetin on Ca^{2+} accumulation in the root of intact rice seedlings	...	106
	28b	The effect of different concentrations of kinetin on Ca^{2+} accumulation in the shoot of intact rice seedlings	...	107
	29a	The effect of different concentrations of kinetin on Mg^{2+} accumulation in the root of intact rice seedlings	...	109
	29b	The effect of different concentrations of kinetin on Mg^{2+} accumulation in the shoot of intact rice seedlings	...	110
	30a	The effect of different concentrations of kinetin on Fe^{2+} accumulation in the root of intact rice seedlings	...	112
	30b	The effect of different concentrations of kinetin on Fe^{2+} accumulation in the shoot of intact rice seedlings	...	113
	31a	The effect of different concentrations of ABA on Cl^{-} accumulation in the root of intact rice seedlings	...	132
	31b	The effect of different concentrations of ABA on Cl^{-} accumulation in the shoot of intact rice seedlings	...	133

Figure	32a	The effect of different concentrations of ABA on NO_3^- accumulation in the root of intact rice seedlings	...	135
	32b	The effect of different concentrations of ABA on NO_3^- accumulation in the shoot of intact rice seedlings	...	136
	33a	The effect of different concentrations of ABA on phosphate accumulation in the root of intact rice seedlings	...	138
	33b	The effect of different concentrations of ABA on phosphate accumulation in the shoot of intact rice seedlings	...	139
	34a	The effect of different concentrations of kinetin on Cl^- accumulation in the root of intact rice seedlings	...	146
	34b	The effect of different concentrations of kinetin on Cl^- accumulation in the shoot of intact rice seedlings	...	148
	35a	The effect of different concentrations of kinetin on NO_3^- accumulation in the root of intact rice seedlings	...	149
	35b	The effect of different concentrations of kinetin on NO_3^- accumulation in the shoot of intact rice seedlings	...	150
	36a	The effect of different concentrations of kinetin on phosphate accumulation in the root of intact rice seedlings	...	152
	36b	The effect of different concentrations of kinetin on phosphate accumulation in the shoot of intact rice seedlings	...	153
	37a	The effect of ABA on the root growth of intact rice seedlings	...	160
	37b	The effect of ABA on the shoot growth of intact rice seedlings	...	162
	38a	The effect of kinetin on the root growth of intact rice seedlings	...	163
	38b	The effect of kinetin on the shoot growth of intact rice seedlings	...	164

Figure 39a The effect of different concentrations of ABA on reducing sugar content in the root of intact rice seedlings ... 174

39b The effect of different concentrations of ABA on reducing sugar content in the shoot of intact rice seedlings ... 176

40a The effect of different concentrations of ABA on total sugar content in the root of intact rice seedlings ... 177

40b The effect of different concentrations of ABA on total sugar content in the shoot of intact rice seedlings ... 179

41 The effect of ABA on (a) H^+ extrusion and (b) K^+ accumulation in the root systems of intact rice seedlings ... 183

LIST OF TABLES

			Page
Table	1	Effect of phytohormones on ion transport process ...	2
	2	The effect of ABA on net influx and long distance transport of K^+ in intact rice seedlings ...	91
	3	The effect of ABA on net influx and long distance transport of Na^+ in intact rice seedlings ...	93
	4	The effect of ABA on net influx and long distance transport of Ca^{2+} in intact rice seedlings ...	95
	5	The effect of ABA on net influx and long distance transport of Mg^{2+} in intact rice seedlings ...	96
	6	The effect of ABA on net influx and long distance transport of Fe^{2+} in intact rice seedlings ...	98
	7	The effect of kinetin on net influx and long distance transport of K^+ in intact rice seedlings ...	114
	8	The effect of kinetin on net influx and long distance transport of Na^+ in intact rice seedlings ...	116
	9	The effect of kinetin on net influx and long distance transport of Ca^{2+} in intact rice seedlings ...	118
	10	The effect of kinetin on net influx and long distance transport of Mg^{2+} in intact rice seedlings ...	120
	11	The effect of kinetin on net influx and long distance transport of Fe^{2+} in intact rice seedlings ...	122
	12	The effect of ABA on net influx and long distance transport of Cl^- in intact rice seedlings ...	141

Table 13 The effect of ABA on net influx and long distance transport of nitrate in intact rice seedlings ... 143

14 The effect of ABA on net influx and long distance transport of phosphate in intact rice seedlings ... 144

15 The effect of kinetin on net influx and long distance transport of Cl^- in intact rice seedlings ... 155

16 The effect of kinetin on net influx and long distance transport of nitrate in intact rice seedlings ... 156

17 The effect of kinetin on net influx and long distance transport of phosphate in intact rice seedlings ... 158

LIST OF PLATES

			Page
Plate	1	Germinated seeds ...	32
	2	Rice seedlings grown in half strength Hoagland solution ...	32
	3	Dunking frame ..	34.
	4	Technique of supporting plants in dunking frame while plant is growing in solution culture ...	34

LIST OF ABBREVIATIONS

ABA	Abscisic acid
BR-10	Cultivar of rice
BA	Benzyladenine
BAP	Benzylaminopurine
CCCP	Carbonyl cyanide-m-chlorophenyl hydrazone
CHM	Cycloheximide
2,4-D	2,4-dichloro-phenoxy acetic acid
2,3-D	2,3-dichloro-phenoxy acetic acid
3,5-D	3,5-dichloro-phenoxy acetic acid
Fe-EDTA	Ethylene diamine tetraacetic acid monoferrous salt
Fc	Fusicoccin
FAP	Furfurylaminopurine
GA	Gibberellic acid
IAA	Indole acetic acid
IBA	indole butyric acid
Jv	Volume flow
KCN	Potassium cyanide
Lp	Hydraulic conductivity
MAP	Methylaminopurine
m.equiv.	Milliequivalent
MP	Membrane electric potential
NAA	Naphthalene acetic acid

Net influx	Net transport of ions through the plasmamembrane
2,4,5-T	2,4,5-trichloro phenoxy acetic acid
Transport index	Long distance transport as percentage of net influx
Ψ_{cx}	Flux of ions from cytoplasm into the xylem
Ψ_{oc}	Flux of ions from outside solution into the cytoplasm

CHAPTER 1

General Introduction

Phytohormone may regulate the internal control mechanism of plant growth through regulation of absorption and translocation of ions. The influence of phytohormones on these physiological phenomenons is dependent on the concentration of hormones, age of plants, types of tissue and the environment of the roots.

The ionic balance in plants changes due to the interaction of phytohormones and inorganic nutrients which affects the growth and development of plants. Thus, phytohormones and inorganic nutrients share a common physiological function, i.e. regulation of growth and development.

Inorganic nutrients control the growth of plants by maintaining the osmotic potential of cells and tissues (Clarkson 1974). Inorganic elements control plant growth by acting as constituents of organic compounds and as co-factor of a number of important biological reactions. Thus, any changes in regulation of ion uptake and distribution in plants will affect the growth of the plants.

A number of reports concerning the effects of auxin, gibberellins, kinetin and abscisic acid (ABA) on the uptake of ions in a wide variety of excised and intact plant tissues have been published (Table I).

Table 1. Effects of phytohormones on ion transport process

Hormone	Effective concentration (M)	Tissue	Ion transport process affected	References
IAA	5.7×10^{-6}	Pea epicotyl segments	Increase in Rb^+ influx	Higinbotham *et al.* (1953)
α-NAA	10^{-5} --- 3×10^{-5}	Intact wheat plants	Inhibition of cation uptake in the order of $K^+ > Na^+ > Mg^{2+} > Ca^{2+}$	Swenson and Burstrom (1960)
IAA	2×10^{-5} - 10^{-4}	Sunflower hypocotyl segments	Increase in K^+ and Rb^+ uptake	Ilan and Reinhold (1963)
ß-IAA	0.1% ß-IAA mixed with lanolin	Decapitated stems of *Pisum sativum*	Stimulation of ^{32}P transport towards IAA-treated apical parts of decapited plants	Davies and Wareing (1965)
IAA	10^{-5}	Sunflower hypocotyl segments	Promotion of H^+ extrusion	Hager *et al.* (1971)
IAA or GA	10^{-5}	Leaf slices of derooted explant pretreated with IAA	Promotion of Cl^- absorption	Kannan and Ramani (1974)
IAA	5×10^{-5}	Potato tuber discs	Partial inhibition of the increased rate of phosphate uptake during aging	Poder *et al.* (1983)
IAA	10^{-3} to 10^{-10}	Isolated maize chloroplasts	Failed to activate Ca^{2+}-ATPase *in vitro*	Maslowski *et al.* (1984)

continued....

Table 1 (continued....)

Hormone	Effective concentration (M)	Tissue	Ion transport process affected	References
IAA	10^{-8}	Young maize seedlings	Slight increase in growth rate, water absorption and cation uptake	Votrubova and Votruba (1986)
IAA and GA	10^{-5} and 10^{-6}	Intact pea plants	Activation of the SO_4^{2-} transport to the upper parts by GA and increases its accumulation in roots by IAA	Zholobak (1985)
GA	10^{-5}	Excised wheat root systems	Initial increase of Cl^- transport and inhibition of K^+ transport	Karmoker and Shaha (1988)
GA_3	10^{-4}	Potato tuber	Decrease in ^{32}P transport	Poder *et al.* (1988)
BA	5×10^{-6}	Bean stem slices	Decrease of K^+ uptake in aged tissue	Rains (1969)
BA/ Kinetin	7×10^{-5}	Beat root discs	Inhibition of K^+ and Na^+ uptake in aged tissue	Van Steveninck (1972a)
BA and Kinetin	5×10^{-8} and 5×10^{-6}	Intact barley plant	Inhibition of K^+ transport in guttation fluid from hydathodes	Dieffenbach *et al.* (1980)
Kinetin	10^{-6}	Isolated maize roots	Decrease of K^+ and Cl^- transport into the xylem	Collins and Kerrigan (1973, 1974)
ABA	1.4×10^{-7}-- 3.8×10^{-5}	*Avena* coleoptile sections	Inhibition of K^+ and Cl^- uptake	Reed and Bonner (1974)

continued....

Table 1 (continued....)

Hormone	Effective concentration (M)	Tissue	Ion transport process affected	References
ABA	10^{-2}	Excised barley roots	Decrease in ^{86}Rb transport into the xylem	Pitman and Wellfare (1978)
ABA	5×10^{-7} to 10^{-4}	Excised bean root systems	7- to 8-fold increase in K^+ and 19- to 20-fold increase in Cl^- transport into the xylem	Karmoker and Van Steveninck (1978)
ABA	10^{-6} to 10^{-4}	Intact *Hordeum vulgare*	Stimulation of K^+ transport in the root and inhibition of its translocation in the shoot	Reidell and Schimid (1984)
ABA	10^{-6}	Culture of *Nostoc* 6720	Increase in intracellular Ca^{2+} content	Smith *et al.* (1987)
Fc	2.5×10^{-5}	Pea internode segments, isolated squash cotyledons	Increase in proton extrusion and K^+ uptake	Marre *et al.* (1975)
Fc	1×10^{-5}	Germinating radish seeds	Stimulation of K^+ uptake	Cocucci and Cocucci (1977)

1.1. Effects of phytohormones on proton pump

The growth rate of *Avena* coleoptile was stimulated by cell elongation in the presence of acid buffer solution (Bonner 1934) and auxin (Pohl 1948). This stimulatory effect was associated with output of protons supported by a cation exchange process.

Cleland (1973) showed that H^+ excretion from *Avena* coleoptile section was rapidly increased by auxin and was inhibited by cycloheximide (CHM), carbonyl cyanide-m-chlorophenyl hydrazone (CCCP) and potassium cyanide (KCN). Canavanine and cordycepin also inhibited H^+ extrusion and K^+ uptake in maize coleoptile (Cocucci and Rossa 1980a, 1980b).

Rayle and Johnson (1973) reported that 2,4-D increased H^+ extrusion but 3,5-D did not increase H^+ extrusion. On the other hand, fusicoccin (FC) stimulated K+ uptake in excised barley roots which was coupled with H^+ extrusion (Pitman *et al.* 1975).

In sunflower hypocotyls, Ilan (1973) observed that depending on the presence of K^+ auxin reduced the pH of external solution. On the other hand, auxin-induced reduction of pH in the external medium showed an association with the auxin-induced growth of hypocotyl segments of *Helianthus annuus* grown in 20 mM Na_2SO_4 (Ilan and Sapira 1976).

Haschke and Luttge (1973) found a 1:1 stoichiometry for indole acetic acid (IAA)-regulated K^+/H^+ exchange in *Avena* coleoptile. But Dijaegere and Neirinckx (1978) did not find 1:1 stoichiometry for K^+/H^+ exchange in barley seedlings.

Zientara (1983) showed that IAA caused a greater hyperpolarization of the membrane potential and large enhancement of the proton pump in wheat coleoptiles. Net H^+ release by isolated protoplasts of rape leaves was also enhanced by IAA but reduced by ABA (Schubert and Matzke 1985). In contrast, Rozers and Hanson (1986) reported that in the non-growing corn root tissue, auxin blocked proton pumping while it increased K^+ influx capacity during developmental phase of washing.

Petzold and co-workers (1988) showed that in the leaf disc of *Vicia faba*, IAA and FC promoted H^+ extrusion while ABA decreased H^+ extrusion. They proposed that the IAA effect is specific. This result supported the view that IAA- and ABA-induced cell growth may be attributed entirely to modulation of H^+ pump activity. The specificity of auxin effect on H^+ extrusion was also supported by Mentze *et al.* (1977).

At low concentration, IAA stimulated H^+ transport in plasma membrane vesicle of tobacco leaves while it inhibited that at higher concentration (Santoni *et al.* 1990).

Peters and Felle (1990) reported that IAA and FC decreased external pH while 2,4-D, 2,3-D, 2,4,5-T, IBA, 1-NAA and 2-NAA stimulated H^+ extrusion in *Zea mays* cleoptile segments.

Alamgir and Maximov (1983) reported that in *Zea mays* seedlings, K^+ absorption was influenced by kinetin which was associated with K^+/H^+ antiport.

Ali-Zade and co-workers (1986) found in root cells of *Trianea bogolensis* that the stimulatory effect of kinetin and inhibitory effect of dicychlohexylcarbodiimide on H^+ excretion increased with an increase in pH of the nutrient solution. The effects were reverse under alkaline condition.

ABA (5×10^{-5} M) caused complete inhibition of auxin-induced H^+ extrusion while it caused partial inhibition at relatively low concentration like 5×10^{-7} M (Rayle 1973).

Karmoker (1981) showed that ABA inhibited H^+ extrusion and K^+ transport in intact bean root systems.

Channa and Collins (1990) reported that ABA increased K^+ flux leaving the H^+ flux little or unaffected in excised roots of *Zea mays*.

Stolarek and Zientara (1991) showed that ABA inhibited H^+ extrusion and K^+ uptake with a simultaneous depolarization of membrane electric potential (MP) while IAA caused substantial acidification of external medium, the highest uptake of K^+ and the largest hyperpolarization of MP in wheat coleoptile segments. GA_3 also increased the above parameters.

1.2. Effects of phytohormones on ion transport in excised plant tissue

Excised plant tissue is an important tool to study ion transport because ion transport occurring in excised tissue does not have

any interference from metabolic and physiological functions operating in the whole plant (Van Steveninck 1975, 1976, 1978).

1.2.1. Effects of auxins on ion transport in excised tissue

A number of reports concerning the effect of auxin on ion transport has been published which explained in terms of cation exchange theory of ion transport. As for example, IAA stimulated K^+ or Rb^+ uptake in sunflower hypocotyl segments which was accompanied by the inhibition of NH_4^+ uptake. Thus, it was suggested by Ilan and Reinhold (1963) that K^+, Rb^+ and NH_4^+ competed for a same carrier site.

IAA stimulated Rb^+ influx into pea epicotyl segments, slices of rutabaga (*Brassica napobrassica*) and potato tuber (Higinbotham *et al.* 1953) and K^+ uptake by sunflower hypocotyl segments (Ilan 1973) and *Mnium* leaves (Luttge *et al.* 1972). On the contrary, Bentrup and co-workers (1973) did not find any effect of IAA on $^{86}Rb/K^+$ influx in root callus cells of *Petroselinum sativum*, while it inhibited ^{36}Cl transport within 30 minutes of application.

IAA stimulated ^{86}Rb uptake within a lag period of 15 to 20 minutes in *Avena* coleoptile sections (Stout *et al.* 1978).

Pfruener and Bentrup (1978) reported that $^{86}Rb/K^+$, ^{22}Na and ^{36}Cl influx was increased in suspension cultured cells of parsley by IAA, and 2,4-D after an initial decrease of apparent influx of these ions occurred within 30 minutes of application. IAA also

stimulated both of K^+ and Na^+ uptake in pea internode segments, but at a low concentration it showed nepotism to K^+ over na^+ (Lado *et al.* 1976).

Zsoldos and Haunold (1982) observed an inhibition of K^+, NH_4^+ and NO_3^- uptake in rice root by 0.01 mM 2,4-D with a low pH in incubation medium. They proposed that at low pH 2,4-D rapidly entered into the root and ultimately ion uptake was inhibited.

Penot and co-workers (1985) reported that in callus cultures derived from the petiole of *Nicotiana tabacum* cv. burley 21, high auxin medium substantially increased K^+ uptake while low auxin medium stimulated K^+ transport to a lesser degree. On the other hand, IAA caused an inhibition of K^+ release from hypocotyl segments of sunflower when it was bathed in 2 mM sodium phosphate buffer (Ilan and Sapira 1979).

De Boer and co-workers (1985) showed that in *Vigna unguiculata* perfusion with IAA and FC caused an stimulation in the electrogenic activity of the xylem pump and also stimulated K^+ uptake from the xylem.

In excised maize roots (Weigal 1969) and beet root discs (Van Steveninck 1974) ^{86}Rb and ^{36}Cl transport was not affected by IAA. On the other hand, ^{36}Cl uptake was substantially increased by α-NAA in coleoptile cells within 15 minutes of application but this stimulatory effect was not found at 0^oC or in the presence of CCCP. This indicated that it was an energy-linked process (Rubinstein 1973, Rubinstein and Light 1973).

Buckhout and co-workers (1981) reported that IAA stimulated the release of Ca^{2+} and Mn^{2+} from membrane pellets of soybean hypocotyls while 2,4-D did not stimulate Ca^{2+} release. They also found that Ca^{2+} release was accompanied by a decrease in Ca^{2+} binding sites in the membrane. On the contrary, Na^{+}, Ca^{2+} and Mg^{2+} content in the soybean stem was decreased by IAA (Castro and Oliviera 1982).

Jones and co-workers (1992) showed that IAA very significantly influenced the rate of Mn^{2+} and some other cations movement into small unilamellar vesicles prepared from soybean phosphatidylinositol (Pi).

IAA inhibited the increased rate of PO_4^{2-} absorption in excised plant tissue (Hourmant and Penot 1978a). Poder and co-workers (1983) also reported that IAA (5×10^{-5} M) partially inhibited the increased rate of PO_4^{2-} uptake during aging of potato tuber discs while FC (10^{-5} M) stimulated it. FC also slightly increased the rate of K^{+} uptake but IAA had no such effect.

Membrane potentiality could be changed by phytohormones in some cases. As for example, Nelles (1977) showed that IAA caused a hyperpolarization in dwarf maize coleoptiles in a few minutes.

1.2.2. Effects of gibberellic acid (GA) on ion transport in excised tissue

Depending on the concentration GA stimulated or inhibited ion transport in excised plant tissue (Van Steveninck 1976, Karmoker 1984). Van Steveninck (1961) showed that 10^{-4} M GA_3 stimulated

the release of K^+ and Na^+ from freshly sliced beet root discs due to increased membrane potentiality by GA_3. At the same concentration GA_3 stimulated both of K^+ uptake and water transport in excised cucumber cotyledons (Ezekiel *et al.* 1978).

Eastwood and Laidman (1971) reported that the release of K^+, Mg^{2+}, Ca^{2+} and inorganic phosphate from germinating embryos was promoted by gibberellin. GA also promoted the release of ions from bean epicotyl (Artinova and Artinova 1971).

Newmann and Jonossy (1977) observed that GA_3 caused an increase in ion content of chloroplast and vacuole but caused no effect on the cytoplasmic ion content in a dwarf maize mutant.

Benllock and co-workers (1983) showed that the addition of GA_3 in nutrient solution did not effect on the exudation process of excised roots while spraying of GA_3 on leaves 2-6 days before excising the root, the rate of exudation and K^+ flux was found to be increased in *Helianthus annuus* cv. Halcon.

GA (10^{-5} M) caused an initial increase of Cl^- transport by 70% in excised wheat root systems while it inhibited K^+ transport (Karmoker and Shaha 1988). On the contrary, Karmoker and Begum (1989) showed that GA stimulated both of K^+ and Cl^- accumulation in the excised root systems of mungbean seedlings.

Hourmant and Penot (1978b) reported that PO_4^{2-} uptake was decreased by GA_3 during the aging of potato tuber discs. On the other hand, the addition of kinetin with GA_3 was essential for

delaying the loss of PO_4^{2-} from senescing leaf segments of barley (Bartolome *et al.* 1981).

Beraud and Penot (1982) observed that GA_3 caused an increase in the initial absorption rate of ^{32}P, SO_4^{2-} and Cl^- by 20-, 9- and 2-fold respectively in the aging tissue of *Pelargonium zonale*.

Israelstam (1987) reported that GA_3 induced greater efflux of inorganic phosphate than control in sweet potato discs. But any difference in uptake rate was not found over the first 10 hours of aging (Israelstam 1983). On the contrary, GA_3 stimulated PO_4^{2-} uptake by 27% in foliar discs of *Pelargonium zonale* (Beraud and Penot 1988).

1.2.3. Effects of abscisic acid (ABA) on ion transport in excised tissue

Reports concerning the effects of ABA on ion transport in excised roots are contradictory. For example, Collins and Kerrigan (1973, 1974) reported that ABA stimulated K^+ flux into the isolated xylem of maize roots. On the contrary, ABA was found to inhibit K^+, ^{86}Rb and Cl^- transport into the xylem of excised barley and maize roots (Pitman and Cram 1973, Pitman *et al.* 1974a, 1974b, Dieffenbach *et al.* 1980).

Horton and Bruce (1972) showed that ABA caused in inhibition of K^+ uptake in leaf discs of *Vicia faba* but had no effect on K^+ transport in leaf discs of mature nonexpanding leaves. On the other hand, ABA stimulated net uptake of K^+, Na^+ and Cl^- in beet root discs (Van Steveninck 1972a).

Karmoker and Van Steveninck (1978) showed that ABA caused an increase in ^{36}Cl and ^{42}K flux into the xylem of excised bean root systems by 19- to 20- and 7- to 8-fold respectively. This stimulatory effect was found to maintain over a period of 48 hours of application. Both of K^+ transport and volume flow was stimulated by ABA over a wide range of concentrations. So, it was proposed that ABA may affect active process of ion transport.

Behl and Jeschke (1979) found an inhibition of K^+ and Na^+ uptake by 93-98% in excised barley roots with 2-3 hours of treatment with ABA. However, tonoplast transport of K^+ and Na^+ in excised barley roots were substantially increased by ABA. That is why a significant decrease of K^+ and Na^+ transport occurred into the xylem (Behl and Jeschke 1981).

Beffagna (1992) reported that ABA caused a decrease in intracellular K^+ contents while it increased Cl^- contents in barley leaf segments. The ABA-induced decrease in intracellular K^+ content was mainly due to the inhibition of K^+ influx while Cl^- uptake did not influenced but Cl^- efflux was inhibited by ABA.

Depending on the concentration ABA was found to stimulate or inhibit transport of ions. For example, at low concentration (0.01 to 0.1 ppm) ABA stimulated Ca^{2+} content in *Lemna gibba*, while it decreased K^+, Ca^{2+} and P content of fronds at high concentration like 1 to 10 ppm (Dekock *et al.* 1978).

Marlo and co-workers (1986) showed that the reabsorption and content of K^+ and Ca^{2+} in the tissue of embryonic axes isolated from *Cicer aerietinum* were rapidly affected by ABA while Na^+ was mobilized more slowly. Reabsorption and content of Mg^{2+} and Mn^{2+} was not affected by ABA. So, it was suggested that ABA mainly affected the osmotic and permeability process.

Smith and co-workers (1987) reported that the intracellular Ca^{2+} content was increased by 20% in the presence of ABA in *Nostoc* 6720.

Karmoker and Van Steveninck (1978) found that ABA at the concentration of 5×10^{-7} M and 10^{-6} M caused 2-fold stimulation of ^{24}Na transport into the xylem of excised bean root systems after 24 hours of treatment. However, vacuolar accumulation of ^{36}Cl and ^{24}Na was increased by 2-fold at 10^{-6} M ABA.

Migliaccio and Rossi (1977) showed that 10^{-5} M ABA stimulated Cl^- and SO_4^{2-} transport into the xylem of excised maize roots at 22°C over a period of 24 hours.

ABA caused an inhibition of P uptake in discs of potato pith (Hamberg 1978) while ABA stimulated NO_3^- accumulation and nitrate reductase activity in fresh potato tuber slices incubated in 0.1-5.0 mM KNO_3 (Palmer 1981).

Maitra and Sen (1987) showed that 10^{-4} M and lower concentrated ABA increased the permeability of leaf cells of cereals.

A relationship exists between ion transport and ABA-induced stomata closure (Mittelheuser and Van Steveninck 1969, 1971, Cummins *et al.* 1971, Kriedemann *et al.* 1972).

Mansfield and Jones (1971) found that ABA inhibited K^+ transport into stomatal guard cells of *Commelina communis* leaves. Horton and Moran (1972) also reported that ABA closed stomata with a concomitant inhibition of K^+ influx into the guard cells of *Vicia faba* leaves.

The effect of ABA on K^+ flux into guard cells might result due to ion exchange (Smith and Raven 1979). For example, in maize the movement of K^+ between guard cells and subsidiary cells was dependent on Cl^- which was an accompanying ion (Raschke and Fellows 1971).

ABA takes part in the regulation of water transport and the ionic balance in plants (Van Steveninck and van Steveninck 1983, Karmoker 1984).

Cram and Pitman (1972) reported that ABA caused inhibition in both water and ion transport from the cut end of barley roots. They proposed that the decrease of water transport was primarily due to an inhibition of ion transport and ABA did not alter the hydraulic conductivity. On the contrary, ABA stimulated water transport in decapitated tomato plants (Tal and Imber 1971), excised sunflower roots (Glinka 1973) and excised maize roots (Collins and Kerrigan 1973, 1974).

Karmoker and Van Steveninck (1978) showed that ABA stimulated water transport in excised bean root systems by 6- to 8-fold. Fiscus (1981) found that in *Phaseolus vulgaris* root systems volume flow (Jv) was initially increased by ABA which was accompanied with an increase in ion transport. The increase in volume flow (Jv) by ABA was due to an increase in hydraulic conductivity (Lp) of the root cell membranes (Glinka and Reinhold 1971, 1972, Glinka 1973).

Behl and Jeschke (1979) observed a substantial decrease in both water and ion transport in excised barley roots. Similar effect was found by ABA in the hypocotyl segments of sunflower (Dorffling 1973) and in barley roots (Cram and Pitman 1972, Pitman and Cram 1973, Pitman *et al.* 1974a, 1974b).

Glinka (1980) showed that ABA caused a rapid decrease in the rate of volume flow and K^+ transport when K^+ was discontinuously supplied in the external medium.

Karmoker and Van Steveninck (1978) reported that in excised bean root systems increase of volume flow was due to an 19- to 20-fold increase in ^{42}K flux into the xylem. They also found that ABA-induced stimulation of both water and ion transport became invalid by CCCP. This indicated the interdependence of water transport and that of ion transport.

Erlandsson and co-workers (1978) found no effect of ABA on water transport while it caused a decrease in ^{86}Rb and ^{32}P transport into the xylem of excised sunflower roots.

Markhart *et al.* (1979) observed that ABA decreased hydraulic conductivity of soybean roots.

1.2.4. Effects of kinetin on ion transport in excised tissue

Kinetin plays an important role in the regulation of ion transport and also takes part in the regulation of water balance in plants. For example, Karmoker (1982) showed that kinetin inhibited volume flow. This inhibition of volume flow was involved with the decrease of ion transport (Collins and Kerrigan 1973, 1974, Glinka 1980, Karmoker 1982).

Van Steveninck (1972b) reported that kinetin and BA inhibited net accumulation of Na^+, K^+ and Cl^- in aged beet root tissue. Similarly, in excised jute root systems, K^+, Na^+ and Cl^- accumulation was inhibited by kinetin (Karmoker and Baten 1992).

Ilan (1971) observed that kinetin stimulated K^+ uptake while it inhibited Na^+ uptake into the leaf discs of *Helianthus annuus.* On the contrary, kinetin decreased K^+ and Cl^- accumulation while it increased Na^+ accumulation in excised roots of rice (Karmoker and Razia 1993).

Humble and Hsiao (1970) showed that kinetin increased K^+ concentration in guard cells. Similarly, BA stimulated both water and K^+ uptake (Ezekiel and co-workers 1978) and K^+ and Na^+ uptake (Prasad and co-workers 1978) in excised cucumber cotyledons.

Ilan and co-workers (1971) reported that kinetin showed a stimulatory effect on K^+, Rb^+ and Cl^- uptake but had no constant influence on Na^+ uptake in detached sunflower cotyledons.

Glinka (1980) observed an inhibitory effect of kinetin on the transport of ions into the xylem of sunflower roots. The inhibitory effect of kinetin was also found in K^+ flux into the xylem of barley roots (Dieffenbach *et al.* 1980) and Rb^+ transport in isolated single roots of honey locust (*Gleditsia triacanthus*).

Karmoker (1982) showed that kinetin caused an inhibition of ^{42}K transport into the xylem of excised bean root systems by 55% after an initial increased. On the other hand, kinetin stimulated the translocation rate of K^+ and K^+/H^+ antiport in the roots of corn seedlings (Alamgir and Maximov 1983).

Collins and Kerrigan (1973, 1974) reported that K^+, Ca^{2+} and Cl^- transport was decreased by kinetin into the xylem of isolated single maize roots.

Elliott and Yuguang (1989) showed that cytokinin initially increased ^{45}Ca accumulation in the protoplast of *Amaranthus tricolor* cotyledons *in vitro* under steady-state conditions (20-40%). *In vivo* application of cytokinin to tissues prior to protoplast isolation also increased Ca^{2+} transport capacity. On the other hand, Ralph and Wojck (1982) did not find any significant effect of kinetin and other cytokinin on ^{45}Ca uptake in corn mitochondria or membrane vesicles.

Kinetin stimulated ATPase activity with Mg^{2+} ions in isolated lupine (*Lupinus luteous*) cotyledons (Przymusinski *et al.* 1981).

Palmer (1976) showed that kinetin inhibited invertase activity and absorption capacity of inorganic phosphate.

Neirinchx (1968) reported that kinetin inhibited SO_4^{2-} absorption which was depended on the selectivity of ion transport process in plants. On the other hand, kinetin inhibited Cl^- and SO_4^{2-} uptake in excised maize roots at 6 hours of treatment but Cl^- efflux was unaffected by kinetin (Migliaccio and Rossi 1977).

1.3. Effects of phytohormones on ion transport in intact plants

Phytohormone was also found to regulate the ion transport in intact plants (Van Steveninck 1976, Karmoker 1984).

1.3.1. Effects of auxins on ion transport in intact plants

In intact plants, auxin caused stimulatory effect on ion transport (Swenson and Burström 1960, Castro and Oliviera 1982) which is opposite to the stimulatory effect of auxins observed in excised plant tissue. Swenson and Burström (1960) found an inhibitory effect of α-NAA on cation uptake in intact wheat plants and an inhibitory series like $K^+ > Na^+ > Mg^{2+} > Ca^{2+}$ were caused by α-NAA. In intact soybean plants Na^+, Ca^{2+} and Mg^{2+} content was also decreased by IAA in the stem (Castro and Oliviera 1982).

Votrubova and Votruba (1986) reported that K^+ uptake, water absorption and growth of maize seedlings was inhibited by high

concentration of IAA (10^{-5} M) but uptake of divalent cation was less affected by IAA. Low concentration of IAA (10^{-8} M) slightly stimulated the growth rate which was accompanied by the stimulation of water absorption and cation uptake. On the other hand, the application of GA or the application of IAA enhanced the entry of SO_4^{2-} into 14-days-old pea plants but the combined application of these two hormones inhibited the entry of SO_4^{2-} (Zholobak 1985).

1.3.2. Effects of gibberellic acid (GA) on ion transport in intact plants

Luttge and co-workers (1968) observed an stimulatory effect of GA on the transport of ions from root to shoot in pea seedlings. On the contrary, GA had no effect on ion transport from root to shoot in intact barley seedlings (Pitman *et al.* 1974a. Dhakal and Erdei (1986a) observed no effect of GA_3 on K^+ and Na^+ uptake in wheat plants.

Starck and Kozinska (1980) observed an stimulatory effect on P and Ca^{2+} content in metabolically active organs and observed on inhibitory effect on the accumulation of Na^+.

Castro and Oliviera (1982) reported that in soybean, K^+ content of leaves and stem and the S content of the stem was stimulated by GA_3 while it inhibited the Ca^{2+} and Mg^{2+} content in the stem. On the other hand, GA_3 stimulated Rb^+ transport to the shoot but did not influence on Rb^+ accumulation in the root of intact *Helianthus annuus* cv. Halcon (Benlloch *et al.* 1983).

Garcia and Guardiola (1981) showed that GA_3 stimulated the uptake of Ca^{2+}, Mg^{2+} and K^+ in seedlings of *Pisum sativum* cv. Progress, while it inhibited the uptake of N and P in cultivars Alaska Progress and Dark Skin Perfection. On the other hand, GA increased K^+ content in primary leaves of bean which was associated with the increase of growth (Stopinska 1987).

GA increased Na^+ content by 20% in roots and increased Na^+ accumulation by 2- to 3-fold in the shoot of intact wheat seedlings (Karmoker and Shaha 1988).

Karmoker and Begum (1989) reported that GA increased both Na^+ and Cl^- content in mungbean leaves but it had no effect on K^+ transport in intact mungbean seedling. GA increased both net influx and long distance transport of Na^+ in intact mungbean seedlings while it decreased long distance transport of K^+ which was associated with the increase of net influx of K^+.

Al-Whaibi and Doaigey (1991) showed that in *Phoenix dactylifera*, nitrogen and partitioning of soluble reducing and total sugars between shoot and root were substantially affected by GA_3 and 2,4-D. On the other hand, Na^+, K^+, Mg^{2+}, Ca^{2+} and P content of both root and shoot were significantly different. So, there should be a relation between growth regulators and ion transport.

1.3.3. Effects of ABA on ion transport in intact plants

ABA caused approximately 49% inhibition of ^{36}Cl transport into the shoot and 19% increase of ^{36}Cl accumulation in the root of intact barley seedlings while it caused an inhibition of K^+ and Cl^- transport into the xylem of excised barley roots (Cram and Pitman 1972). Shanner and co-workers (1975) also found an inhibition of K^+ uptake both in excised maize roots and intact seedlings. On the contrary, Pandey and Kannan (1976) observed that ABA stimulated the movement of ^{86}Rb and ^{59}Fe from the primary leaves to the roots in bean plants. Similarly, it was found that ABA increased the transport of Fe^{2+} from root to the trifoliate leaves.

Karmoker and Van Steveninck (1978) observed vast difference between intact and excised bean with respect to K^+ transport by ABA. They recorded substantial inhibition of ^{42}K transport by ABA in intact bean seedlings while ABA caused a substantial increase in ^{42}K transport into the xylem of excised bean root systems. They also reported that Na^+ and Cl^- accumulation was increased in intact bean root while that of K^+ was decreased by ABA. On the other hand, the net influx of Cl^- and Na^+ either increased or remained constant under the influence of ABA in intact seedlings while at the same time fluxes of these ions into root vacuole were increased (Karmoker and Van Steveninck 1979a).

Dieffenbach and co-workers (1980) found that ABA decreased K^+ transport in the guttation fluid from passive hydathods after an initial increase in intact barley seedlings. On the other hand, ABA stimulated K^+ transport into roots while it inhibited translocation of ions to the shoots (Riedell and Schimid 1984).

Dhakal and Erdei (1986b) reported that ABA decreased K^+ and Na^+ level more effectively in high K^+ than in low K^+ young wheat plants.

Gunvor and co-workers (1990) reported that ABA, at a concentration of 40-80 μM inhibited K^+ (^{86}Rb) influx in 7-days-old wheat seedlings but temporary stimulation of K^+ (^{86}Rb) influx was found by pretreatment of the plants with ABA. They also observed that accumulation of Na^+ and Cl^- was increased while K^+ accumulation was decreased in intact roots by ABA. On the other hand, ABA at a higher concentration increased NO_3^- content but decreased K^+ and PO_4^{2-} content while low concentration of ABA increased Ca^{2+} uptake in *Lemna gibba* (Dekock ***et al.*** 1978).

Poder and co-workers (1988) reported that ABA did not change the distribution of ^{32}P within the plant while foliar spray with ABA largely increased the transport ^{32}P into the tuber of *Solanum tuberosum*.

Jacoby and Dagan (1970) found that benzyladenine (BA) inhibited the rate of Na^+ absorption in expanding primary leaves of intact bean plants while it stimulated the transport of Rb^+ and Fe^{2+} from leaves to the roots of bean.

Karmoker and Van Steveninck (1979b) observed a relationship between the effect of ABA on sugar level and ion transport. They reported that 10^{-6} M ABA increased reducing sugar content and total sugar content in the root of intact bean seedlings by 3-fold and 86% respectively but did not have any effect on excised root of bean. This result indicated that ABA increase the transport of sugar from the shoot to the root. The increase of sugar level in intact roots of bean seedling may be related with an inhibition of ion transport by ABA (Karmoker and Van Steveninck 1979a). The relationship between sugar level and ion transport in barley roots was also supported by Pitman *et al.* (1971).

1.3.4. Effects of kinetin on ion transport in intact plants

Pandey and Kannan (1976) reported that kinetin stimulated the transport of Fe^{2+} from root to the primary and trifoliate leaves when it was supplied to the root.

Karmoker (1981) showed that the uptake and transport of ^{22}Na, ^{36}Cl and ^{42}K was inhibited by kinetin in intact bean seedlings which was similar to that of in excised root systems. Kinetin with BA also decreased the transport of K^+ in the guttation fluid of intact barley seedlings (Dieffenbach *et al.* 1980).

Bittner and Buschmann (1983) reported that kinetin reduced the uptake of K^+ and Ca^{2+} in the root of intact radish seedlings but it did not change the relative distribution of the ions in cotyledons, hypocotyl and root. On the other hand, depending on

the concentration of used kinins, some of its analogues slightly inhibited K^+ and phosphorus transport in intact pumpkin (Abutalybov *et al.* 1975).

Kinetin also caused a decrease in the PO_4^{2-} of the cellular mass and was observed in *Chlorella pyrenoidosa* cultivars (Torre and Liliana 1987).

Karmoker and Baten (1992) reported that kinetin stimulated the accumulation of K^+, Na^+ and Cl^- in roots of intact jute seedlings while it inhibited the accumulation of those ion in excised jute root systems. They also reported that kinetin inhibited both K^+ and Cl^- accumulation but stimulated Na^+ accumulation in the shoot. Net influx and long distance transport of K^+, Na^+ and Cl^- was also increased by kinetin.

Karmoker and Razia (1993) showed that kinetin decreased K^+ transport in the root and shoot and increased Na^+ and Cl^- accumulation in the root of intact rice seedlings. But the transport of Na^+ and Cl^- in the shoot was inhibited by kinetin.

The reports on the effect of phytohormone on divalent ions are very rare. Besides, effect of phytohormone on ion transport in rice (*Oryza sativa* L.) is also rare. Hence, rice seedling was chosen for the experiment.

The aim of present investigation was to study:

1) Regulatory aspects of phytohormone-directed ion transport: In this respect the effect of kinetin and abscisic acid

(ABA) on uptake and transport of divalent ions in excised roots and in intact rice seedlings, and (b) uptake and transport of monovalent ions were also studied.

2) Mechanistic aspects of phytohormone directed ion transport: In this respect the effect of kinetin and abscisic acid (ABA) on H^+ excretion, sugar level and its correlation with ion transport was studied.

CHAPTER 2

Materials and Methods

2.1. Plant Materials

In the present investigation *Oryza sativa* L. cv. BR-10 was used as plant materials. Seeds of BR-10 were obtained through the courtesy of Bangladesh Rice Research Institute (BRRI) at Gazipur.

2.2. Solution Culture Technique

Plants were grown in half strength Hoagland solution (Hoagland and Arnon 1950). The composition of modified full strength Hoagland solution was as follows:

a) Micronutrients

46.25 μM H_3BO_3, 9.15 μM $MnCl_2.4H_2O$, 0.81 μM $ZnCl_2$, 0.29 μM $CuCl_2.2H_2O$ and 0.10 μM $Na_2MoO_4.2H_2O$ were used as micronutrients.

b) Macronutrients

5 μM $Ca(NO_3)_2.4H_2O$, 5 μM KNO_3, 2 μM $MgSO_4.7H_2O$, 1 μM KH_2PO_4 and 1 μM Fe-EDTA were used as macronutrients.

2.3. Preparation of Stock Solution

2.3.1. Stock solution of micronutrients

Distilled water (600-700 ml) was taken in a one-litre volumetric flask. Then inorganic compounds as listed below were added to it one by one and shaken well in between. After dissolving all the compounds, the content of the flask was made up to the final volume of one litre by adding distilled water.

Inorganic compounds		Amount of inorganic compound dissolved in one litre of solution (gm)
H_3BO_3	...	2.86
$MnCl_2.4H_2O$	...	1.81
$ZnCl_2$	...	0.11
$CuCl_2.2H_2O$	...	0.05
$Na_2MoO_4.2H_2O$	...	0.25

2.3.2. Stock solution of macronutrients

Stock solution of macronutrients were prepared separately according to following composition. To prepare each macronutrient solution, approximately 600 ml of distilled water was taken in a one-litre volumetric flask. The prescribed amount of inorganic compound was added to it and shaken in between. The content was made up to a final volume of one litre by adding distilled water.

Concentration of inorganic compounds		Amount of inorganic compound dissolved (g/l)
1 M $Ca(NO_3)_2.4H_2O$	...	236.15
1 KNO_3	...	101.11
1 M $MgSO_4.7H_2O$	...	246.47
1 M KH_2PO_4	...	136.09
0.1 M Fe-EDTA	...	36.71

2.3.3. Preparation of full strength Hoagland solution

Distilled water (600-700 ml) was taken in a one-litre volumetric flask. Then micronutrient and macronutrient stock solutions as listed below were added to the volumetric flask one by one and shaken in between. The content was made up to a final volume of one litre by adding distilled water.

Stock solution		ml/l
a) Micronutrient	...	1.0
b) Macronutrients		
1 M $Ca(NO_3)_2.4H_2O$	...	5.0
1 M KNO_3	...	5.0
1 M $MgSO_4.7H_2O$	...	2.0
1 M KH_2PO_4	...	1.0
0.1 M Fe-EDTA	...	1.0

Plates were grown in half strength Hoagland solution. The pH of half strength Hoagland solution was 5.5 to 6.0.

2.3.4. Stock solution of abscisic acid (ABA)

0.002643 gm ABA was taken in 50 ml distilled water in a conical flask of 250 ml capacity covered by aluminum foil to avoid degeneration by sunlight. The flask was shaken overnight in a shaker (Model BXS, Mitamura Rika Kogyo Inc., Tokyo, Japan). The content was made up to a final volume of 250 ml with distilled water. Thus, 4×10^{-5} M stock solution of ABA was prepared.

2.3.5. Stock solution of kinetin

0.001076 gm kinetin was taken in a test tube. One ml of propylene glycol was added to it and stirred with a magnetic stirrer until kinetin was dissolved. The dissolved kinetin was then taken in a 250 ml volumetric flask and made up to a final volume of 250 ml with distilled water. Thus, 2×10^{-5} M stock solution of kinetin was prepared.

2.4. Culture of Plants

2.4.1. Surface sterilization of seeds

In order to avoid fungal infection, surface of seeds were sterilized with 0.1% $HgCl_2$ solution for one minute. $HgCl_2$-treated seeds were washed under tap water for several times (7-12 times). The seeds were finally washed with distilled water for 3 to 4 times. Before sowing, the seeds were soaked in distilled water for 30 minutes and continuously air was passed with the help of air compressor (Model Compton Com/VAG. PUMP, Type

D/351VM, W/O. No. 30100, Serial No. S5062, Dawson McDonald and Dawson, Ltd., Ashbourne, Derbyshire).

2.4.2. Growing of plants in solution culture

Surface sterilized seeds were spread on cotton gauze on a perforated plastic cover fitted to a Pyrex glass beaker of 500 ml capacity filled with half strength Hoagland solution. The beaker was painted black to prevent the roots being exposed to light. The nutrient solution was taken in a beaker to such a level that the cotton gauze was just in contact with the solution. Two pieces of cotton gauze were inserted into the nutrient solution through the holes of the plastic cover so that the cotton gauze remained wet all the time to keep the germinating seeds wet.

Beaker with the sown seeds was kept in the natural environment in dark during germination. Seeds were germinated within 48 hours of sowing (Plate 1). The beaker with the seedlings was transferred to a growth chamber (Model EA-7BH, Environmental Air, Sydney, Australia).

Growth condition of the cabinet was as follows: Day temperature was $30\pm1^{o}C$ and night temperature was $25\pm1^{o}C$. Day and night lengths were 14 and 10 hours, respectively. Relative humidity was 80% by day and 90% by night.

The solution of the beaker was aerated with the help of an air compressor.

Plate 1. Germinated seeds

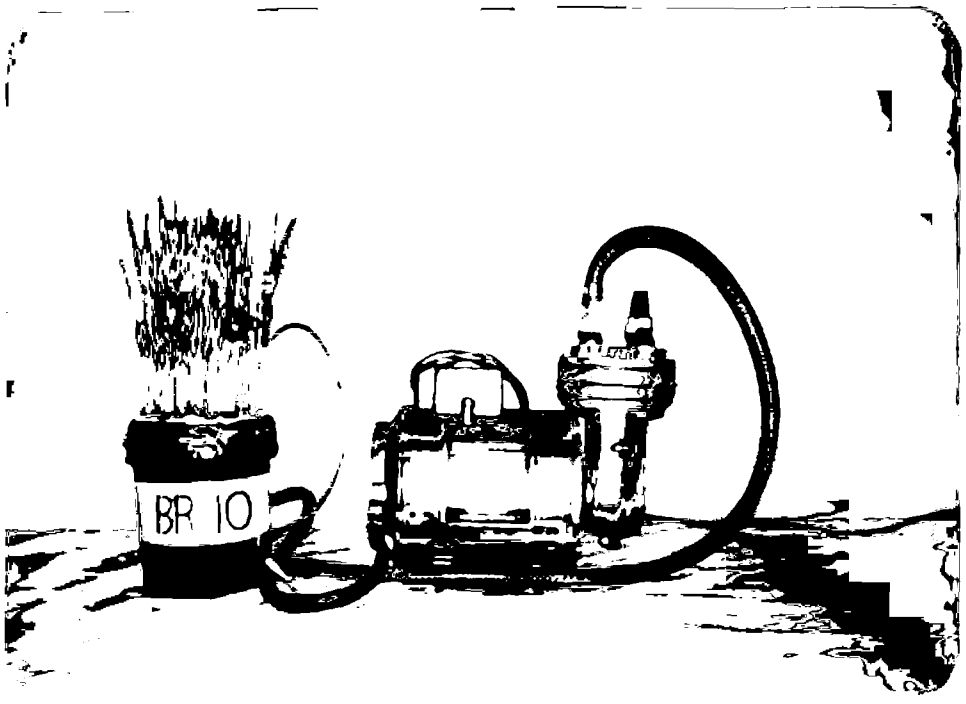

Plate 2. Rice seedlings grown in half strength Hoagland solution

2.5. Ion Transport Experiment with Excised Root Systems

Ten-days-old seedlings (Plate 2) were decapitated at 1 cm above apparent root-stem junction. The decapitated roots were then fixed into dunking frame (Plate 3) with a strip of insulin tape and transferred to a beaker containing half Hoagland solution with or without hormones. The experimental solution was aerated continuously by an air compressor.

2.6. Ion Transport Experiment with Intact Plants

Ten-days-old seedlings (Plate 2) were selected and were fixed into dunking frame (Plate 3) with a strip of insulin tape which was then transferred to a beaker containing half Hoagland solution with or without hormone (Plate 4). The experimental solution was aerated continuously by an air compressor.

2.7. Collection and Drying of Samples

Root and shoot samples were collected at 3, 6, 24 and 48 hours of treatment. The root systems were separated from the shoot in case of intact plant. Roots of intact plants and excised roots were washed in two changes of 0.2 mM $CaSO_4$ for 5 minutes to remove free space ions (Karmoker 1981). The root systems were blotted.

The root and shoot samples were dried in an oven at $80^{o}C$ for 48 hours. Then the dry weight of the samples were recorded with an electronic balance (FR-200).

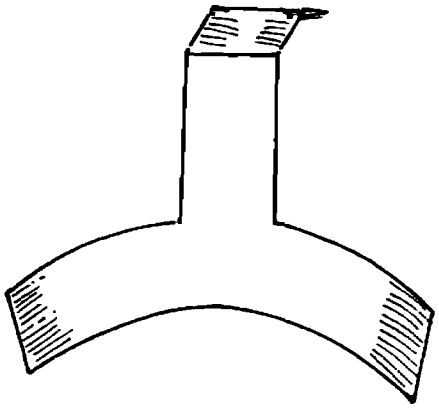

Plate 3. Dunking frame

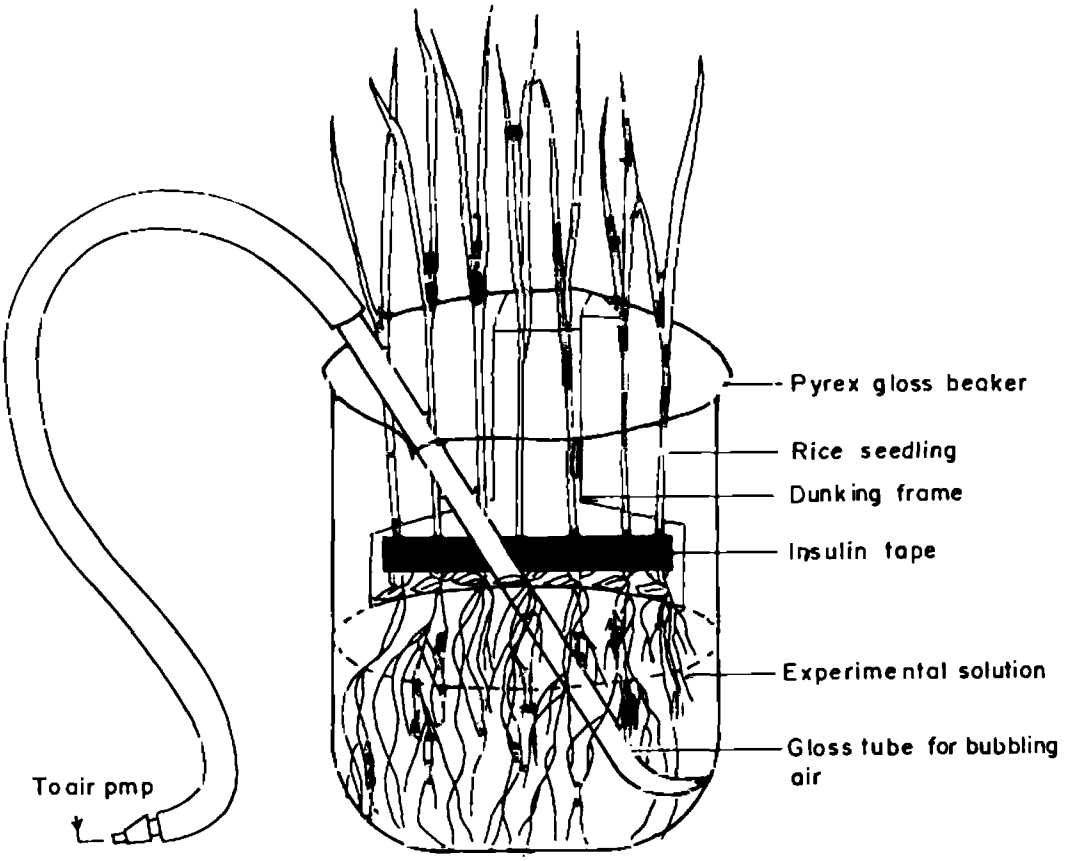

Plate 4. Technique of supporting plants in dunking frame while plant is growing in solution culture

2.8. Methods of Extraction and Measurement of Ions in Plant Tissue

2.8.1. Extraction of K^+, Na^+, Ca^{2+}, Mg^{2+}, Fe^{2+} and phosphate

After recording dry weight, the samples were taken in test tube separately. 4 ml mixture of concentrated HNO_3 and $HClO_4$ (4:1 ratio) was added to the test tube and allowed to stand for 30 minutes. The test tubes with the samples and acid mixture were heated in a sand bath in order to digest the tissue. The extract was evaporated almost to dryness. The extract was then diluted to a final volume of 20 ml with distilled water.

2.8.2. Extraction of chloride and nitrate

In order to extract total amount of chloride (Cl^-) and nitrate (NO_3^-), the root and the shoot samples (after recording the dry weight) were taken separately in test tubes. Samples were soaked in 10 ml of distilled water for 30 minutes and then boiled in a water bath for 30 minutes. The extract was collected in another test tube. Another 5 ml of distilled water was added to the residue and boiled for 15 minutes and extract was collected. Again 5 ml of distilled water was added to the residue and boiled for another 10 minutes and extract was collected. Finally, the combined extract was made up to a final volume of 20 ml.

2.8.3. Measurement of K^+ and Na^+

The uptake of K^+ and na^+ by plant tissue was measured using a Flame Photometer (Model ANA-I0KL, Tokyo Photoelectric Co., Ltd., Japan) at wavelength of 767 and 589 nm respectively. Concentration of K^+ and Na^+ in the extract (ppm) was determined with the help of a standard curve as shown in Fig. 1 and Fig. 2 respectively.

The amount of K^+ and Na^+ were calculated using the following formula:

$$\text{Ion content} = \frac{\text{Concentration of ion in the extract (ppm)} \times \text{Final volume of the plant extract (ml)}}{\text{Dry weight of the tissue} \times \text{Atomic weight of the respective ion} \times 1000}$$

$$= X \text{ m. equivalent } g^{-1} \text{ dry tissue}$$

2.8.4. Measurement of Ca^{2+}, Mg^{2+} and Fe^{2+}

The uptake of Ca^{2+}, Mg^{2+} and Fe^{2+} was measured using an atomic absorption spectrophotometer (Model PYE UNICUM SP9) at wavelengths of 285.2, 422.7 and 248.3 respectively.

Concentration of Ca^{2+}, Mg^{2+} and Fe^{2+} in the extract (ppm) was determined with the help of standard curve as shown in Fig. 3, Fig. 4 and Fig. 5 respectively.

The amount of Ca^{2+}, Mg^{2+} and Fe^{2+} were calculated using the following formula:

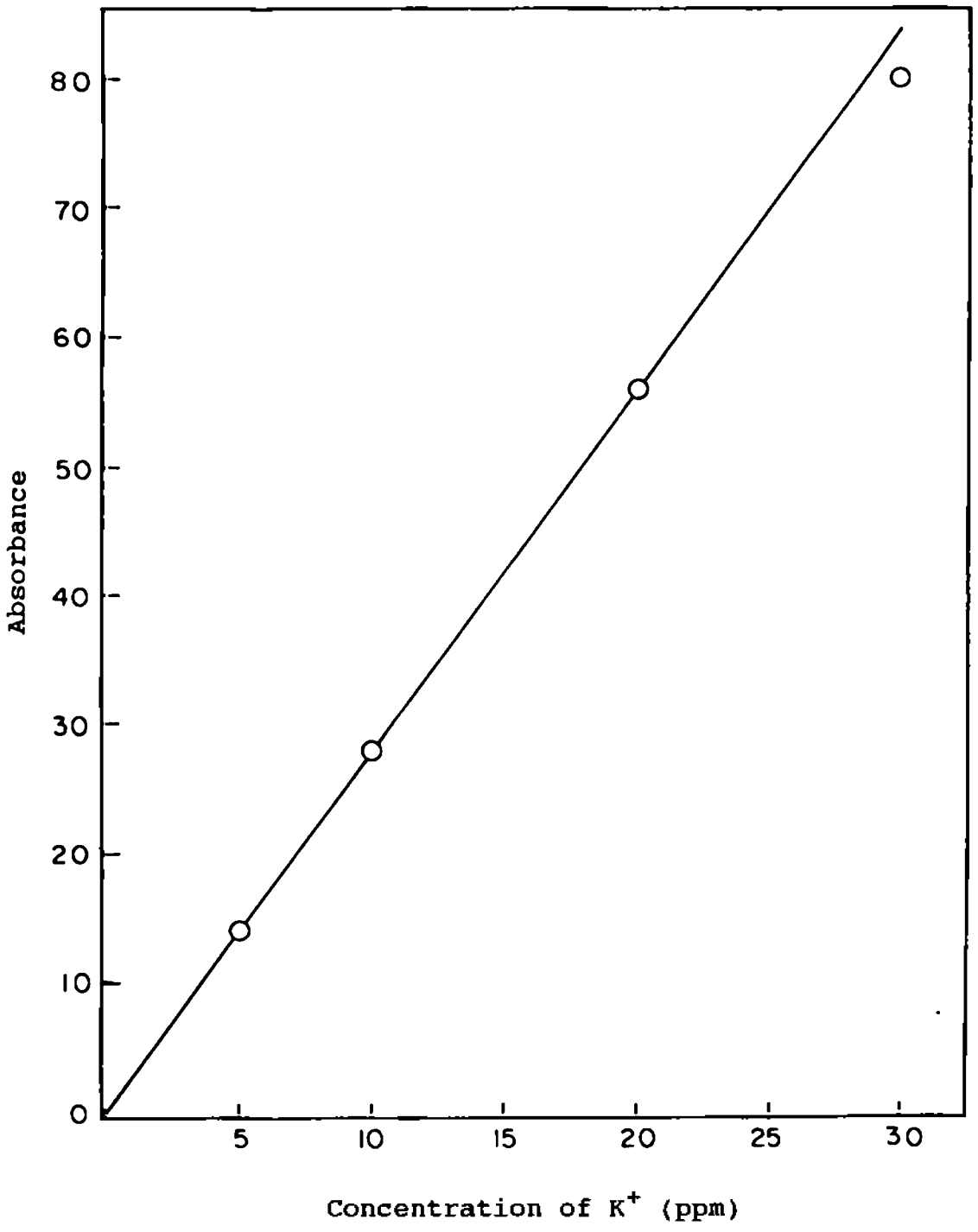

Fig. 1. Standard curve for potassium

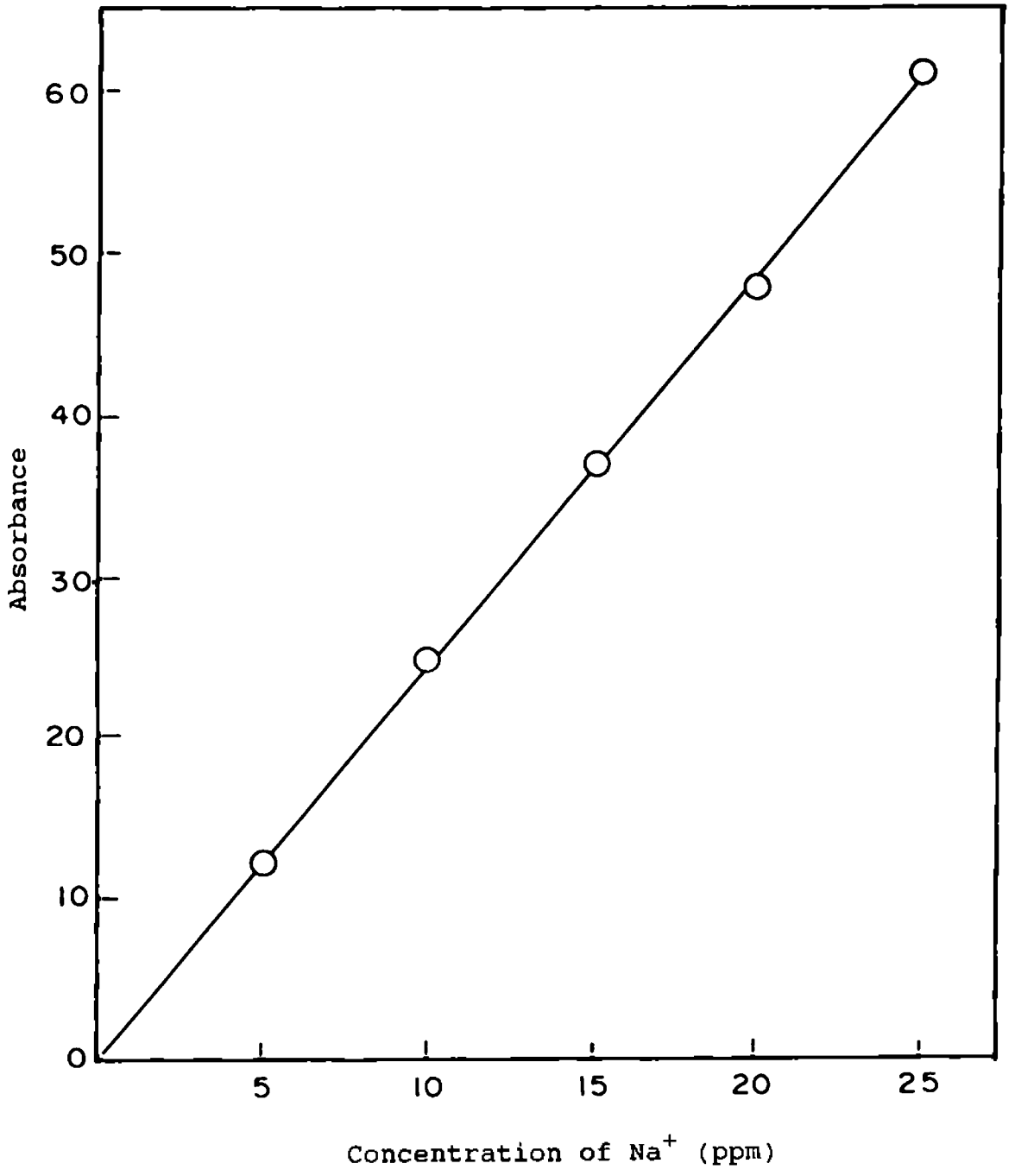

Fig. 2. Standard curve for sodium

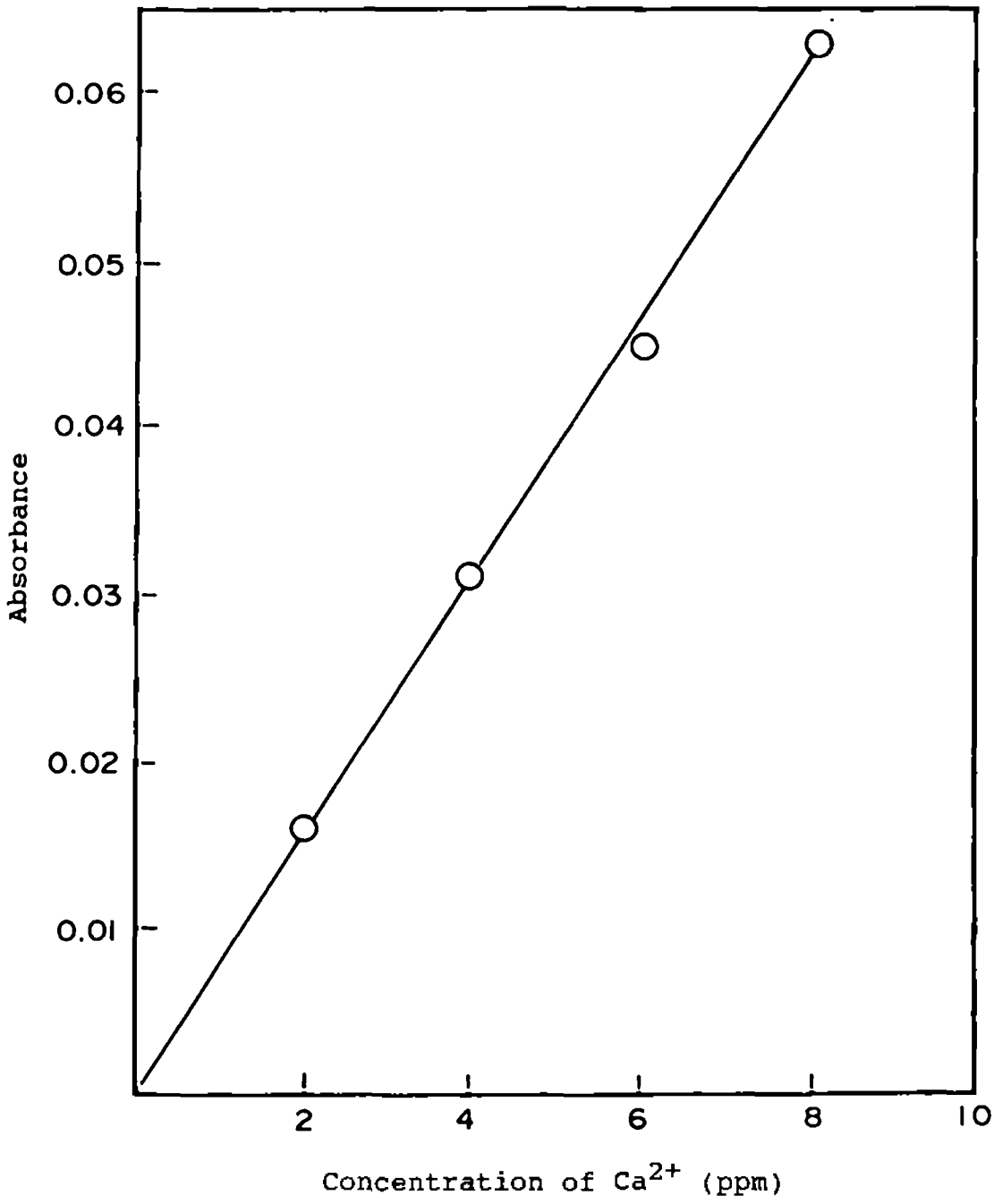

Fig. 3. Standard curve for calcium

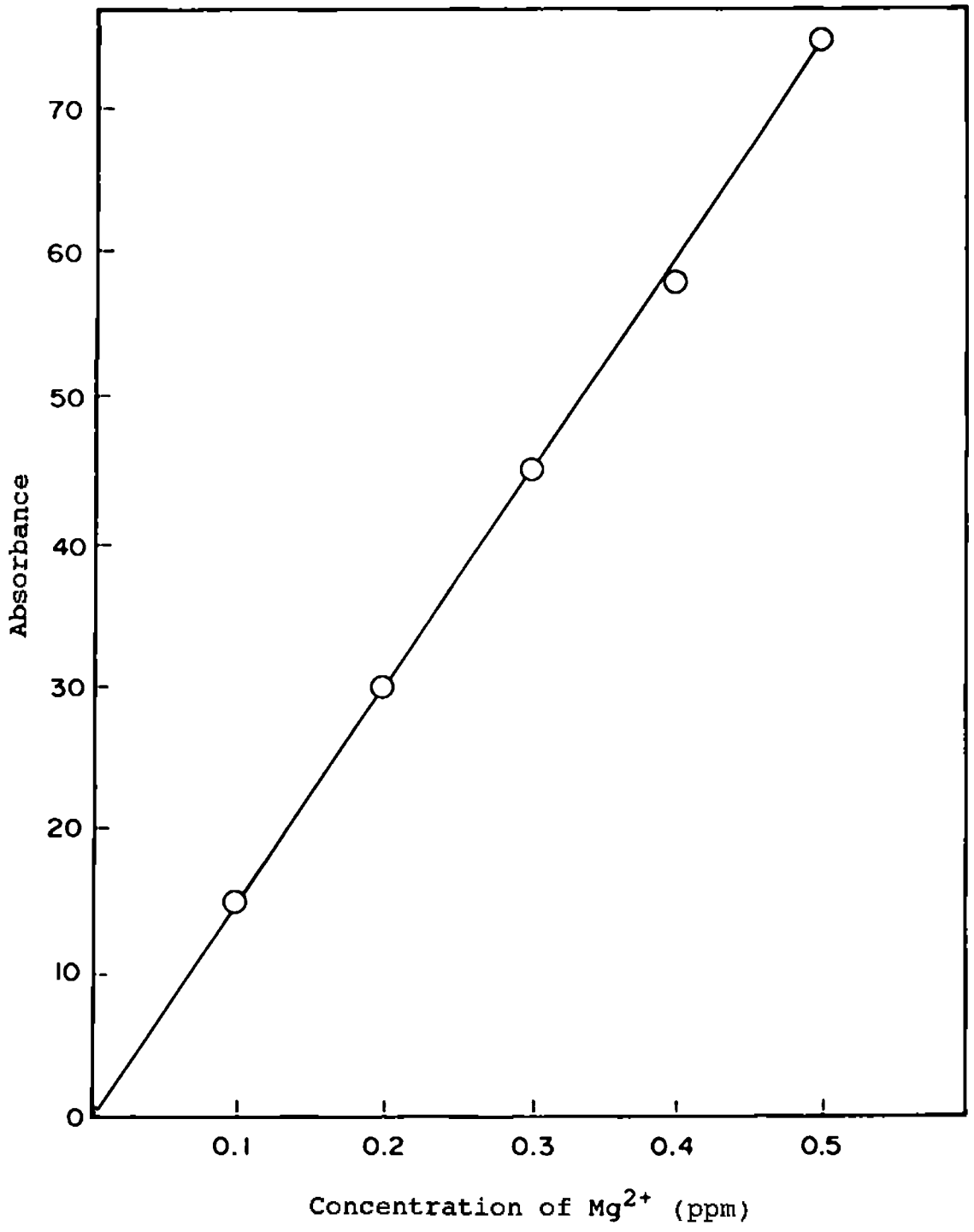

Fig. 4. Standard curve for magnesium

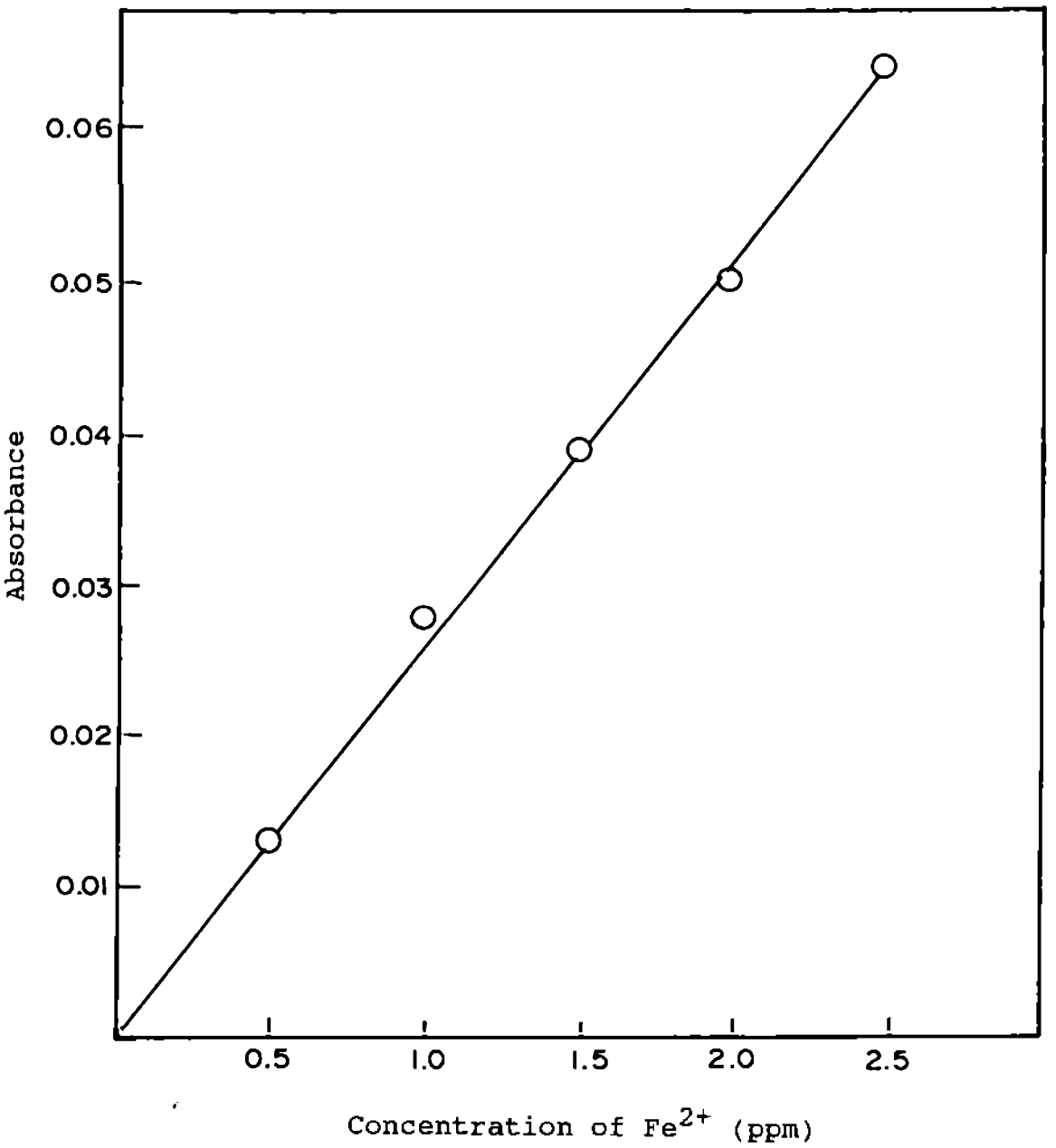

Fig. 5. Standard curve for iron

$$\text{Ion content} = \frac{\text{Concentration of ion in the extract (ppm)} \times \text{Final volume of the plant extract (ml)}}{\text{Dry weight of the tissue} \times \text{Atomic weight of the respective ion} \times 1000}$$

$$= X \text{ m. equivalent } g^{-1} \text{ dry tissue}$$

2.8.5. Measurement of Cl^-

Amount of Cl^- in plant tissue was measured by titrametric method. 5 ml of extract was titrated with 0.05 N $AgNO_3$ using potassium chromate (K_2CrO_4) as an indicator.

The concentration of Cl^- in the extract (ppm) was determined using a standard curve for Cl^- (Fig. 6).

The amount of Cl^- in the tissue was calculated using the following formula:

$$Cl^- \text{ content} = \frac{\text{Amount of } Cl^- \text{ in 0.05 N solution} \times \text{Normality of extract} \times \text{Final volume of extract} \times \text{Atomic weight of } Cl^-}{\text{Dry weight of tissue} \times \text{Atomic weight of the } Cl^- \times 1000}$$

$$= X \text{ m. equivalent } g^{-1} \text{ dry tissue}$$

2.8.6. Measurement of nitrate

Nitrate (NO_3^-) was measured by salicylic acid method (Cataldo *et al.* 1975).

2.8.6.1. Preparation of 5% salicylic acid

Five gram of salicylic acid (SA-H_2SO_4) was taken in 50 ml (approximately) of H_2SO_4 in a conical flask of 100 ml capacity.

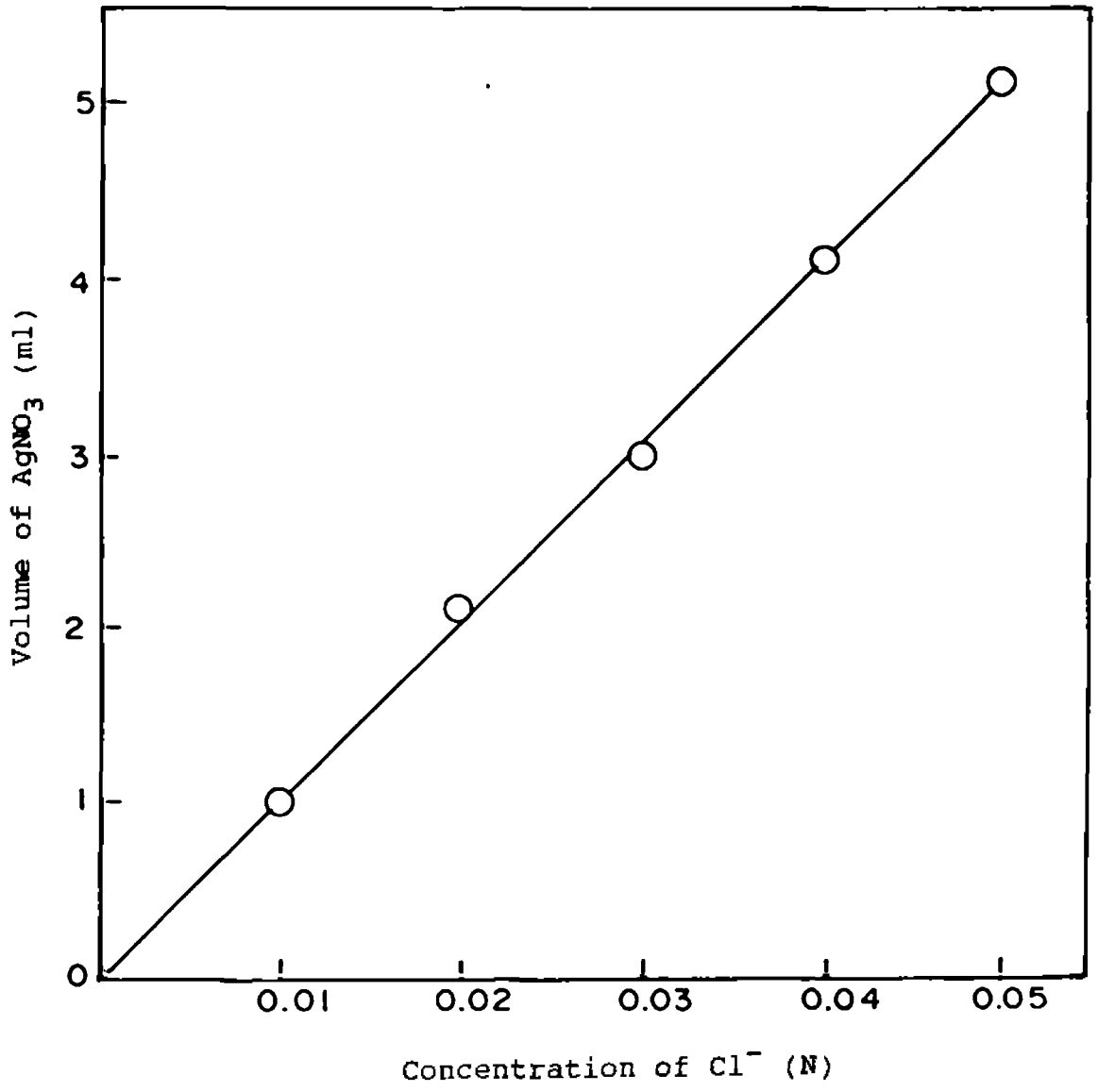

Fig. 6. Standard curve for chloride

After dissolving salicylic acid the content was made up to a final volume of 100 ml with H_2SO_4. Thus, 5% (w/v) salicylic acid was prepared. The SA-H_2SO_4 reagent was made fresh at least once each week and stored in brown bottle.

2.8.6.2. Preparation of 2N NaOH solution

Eighty gram of NaOH was taken in 500-600 ml distilled water. The flask was shaken well. After dissolving NaOH the content was made up to a final volume of 1000 ml with distilled water. Thus, 2N NaOH was prepared. 2N NaOH was added to distilled water gradually while dissolving it.

2.8.6.3. Determination of nitrate

In order to measure NO_3^- in plant tissue, 0.2 ml of extract was taken in 50 ml Erlenmeyer flask and 0.8 ml of 5% SA-H_2SO_4 was added to it. The content of the flask was mixed thoroughly and allowed to stand for 20 minutes at room temperature. 19 ml of 2N NaOH was added slowly to raise the pH above 12.0. Samples were cooled at room temperature.

0.2 ml of standard solution (which was stored at 4^oC) was taken and similarly above reagent was mixed to it. A blank was also run where 0.2 ml of distilled water was taken.

Finally, absorbance of NO_3^- was measured at 410 nm wavelength with the help of a spectrophotometer (Model AnA-72, Tokyo Photoelectric Co., Ltd., Japan).

The concentration of NO_3^- (ppm) in the extract was determined using a standard curve for NO_3^- (Fig. 7).

The amount of NO_3^- in the plant tissue was calculated by using the following formula:

$$NO_3^- \text{ content} = \frac{\text{Concentration of } NO_3^- \text{ in the extract (ppm)} \times \text{Final volume of the plant extract (ml)}}{\text{Dry weight of the tissue} \times \text{Atomic weight of } NO_3^-} \times 1000$$

$$= X \text{ m. equivalent } g^{-1} \text{ dry tissue}$$

2.8.7. Measurement of phosphate

Phosphate was measured by Vando Molybdate Phosphoric Yellow Colour method (Jackson 1967). In order to measure phosphate different types of solution were prepared.

2.8.7.1. Preparation of solution A

Twenty-five gram of ammonium molybdate was taken in 400 ml of distilled water. The solution was heated and cooled at room temperature.

2.8.7.2. Preparation of solution B

1.25 gm ammonium metavanadate was taken in 300 ml of boiling water and cooled at room temperature. Then 250 ml of concentrated HNO_3 was added to it and again cooled at room temperature.

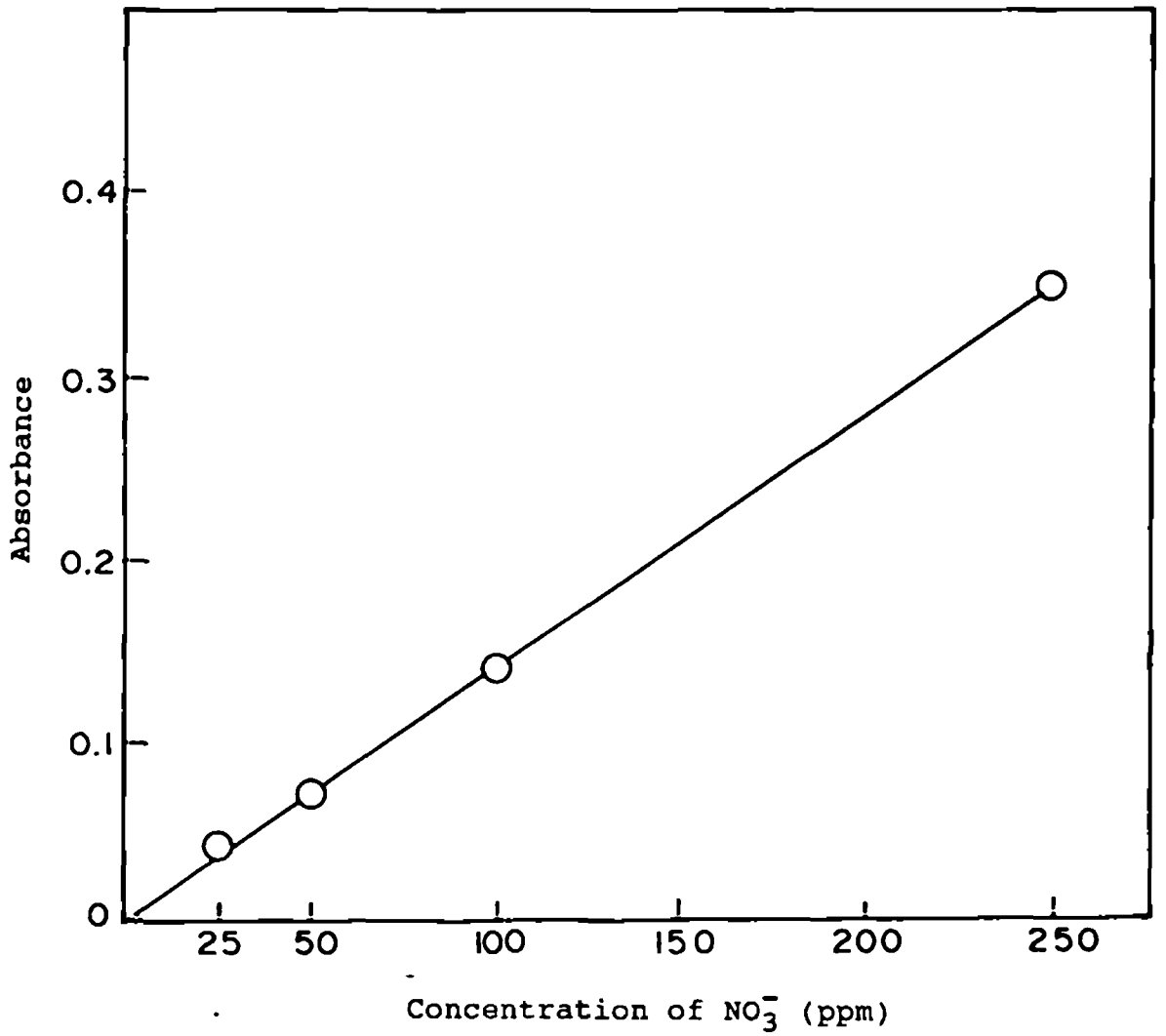

Fig. 7. Standard curve for nitrate

2.8.7.3. Preparation of solution C

Solution C was prepared just before use. To prepare solution C, solution A, solution B and distilled water were taken at a ratio of 4:5.5:0.5 and mixed thoroughly.

2.8.7.4. Determination of phosphate

Ten ml of extract was taken in a test tube and 10 ml of solution C were added to it to develop yellow colour and then allowed to stand for 10 minutes. Finally, absorbance of phosphate was measured at 440 nm wavelength with spectrophotometer (Model AnA-72, Tokyo Photoelectric Co., Ltd., Japan).

The concentration of phosphate in the extract was calculated using a standard curve for phosphate (Fig. 8).

The amount of phosphate in the plant tissue was calculated using the following formula:

$$\text{Phoapate content} = \frac{\text{Concentration of phosphate in the extract (ppm)} \times \text{Total volume of the content (ml)} \times \text{Final volume of extract (ml)}}{\text{Amount of extract taken (ml)} \times \text{Dry weight of the tissue (gm)} \times \text{Atomic weight of phosphate} \times 1000}$$

$$= X \text{ m. equivalent } g^{-1} \text{ dry tissue}$$

2.9. Methods of Extraction and Measurement of Sugar

2.9.1. Extraction of sugar

The fresh tissue (after recording the fresh weight) was taken separately in test tube and boiled in 5 ml of 80% ethanol for 5

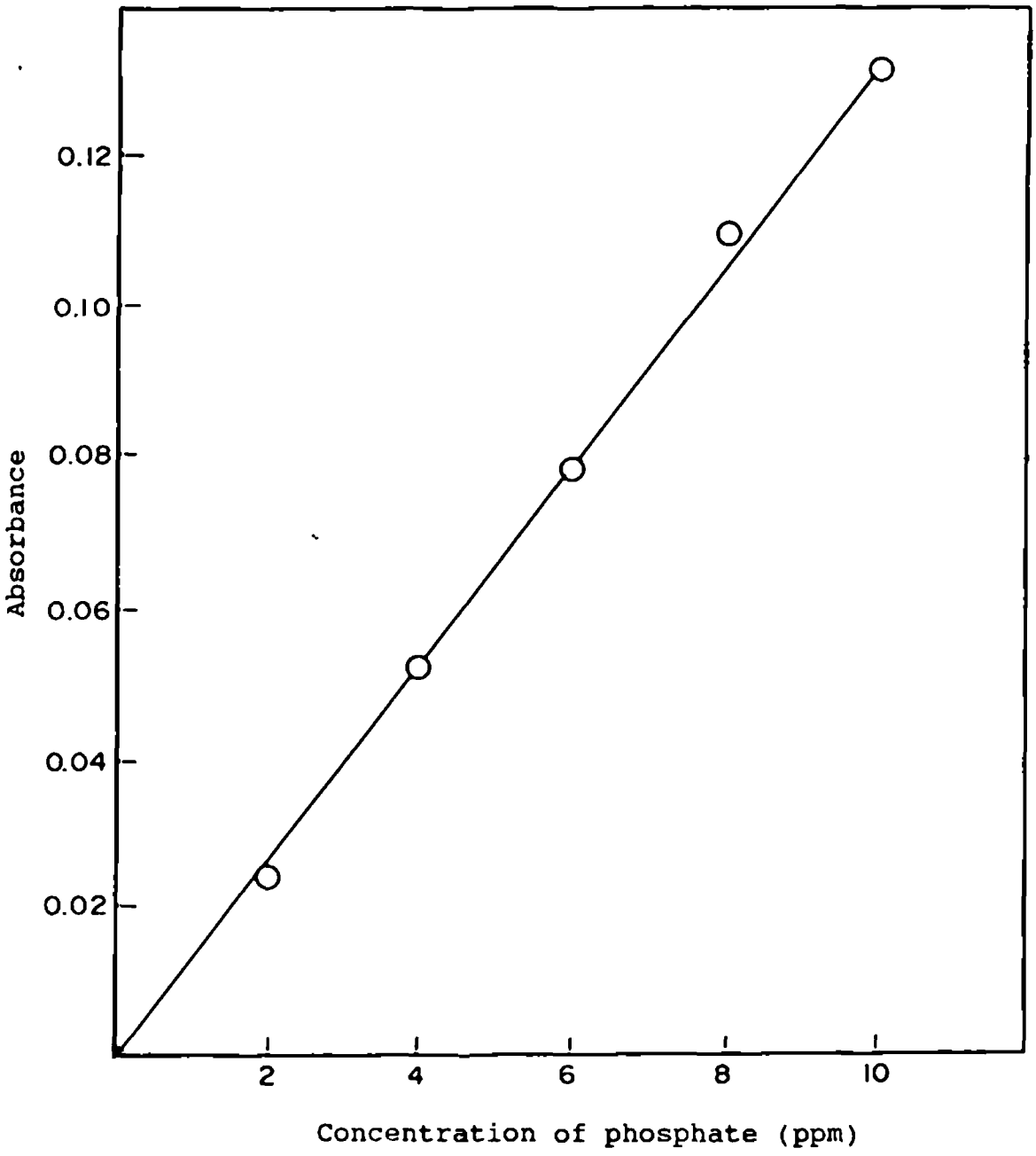

Fig. 8. Standard curve for phosphate

minutes. It was repeated with further change of 5 ml of 80% ethanol. Then the extract was evaporated to approximately 3 ml in a graduated 50 ml beaker to remove the alcohol. In the case of root, extract was diluted to 15 ml with distilled water. But in case of shoot, extract was partitioned twice with the mixture of 80% alcohol and petroleum-spirit (bp 40-60) at 1:2 ratio to remove chlorophyll. Then it was evaporated to approximately 3 ml and diluted to 30 ml with distilled water.

2.9.2. Measurement of reducing sugar

Reducing sugar was measured by the Somogyi-Nelson method (Nelson 1944, Somogyi 1952). Different types of stock solution was prepared for the measurement of reducing sugar.

2.9.2.1. Preparation of solution I

Eight hundred ml of distilled water was taken in a volumetric flask and 15 gm K-Na tartrate, 30 gm Na_2CO_3, 20 gm $NaHCO_3$, 180 gm Na_2SO_4 were added and shaken in between. Na_2SO_4 was gradually added to distilled water while dissolving it. The solution was made up to a final volume of 1000 ml with distilled water.

2.9.2.2. Preparation of solution II

In order to prepare solution II, 5 gm $CuSO_4.5H_2O$ and 45 gm Na_2SO_4 were dissolved in 250 ml distilled water.

2.9.2.3. Preparation of solution III

Just prior to use, four parts of solution I was mixed with one part of solution II.

2.9.2.4. Preparation of arsenomolybdate

Twenty-five gram of ammonium molybdate was dissolved in 450 ml of distilled water. Twenty-one ml of concentrated H_2SO_4 was added to it and mixed well. Then 3 gm sodium arsenate was added, dissolved in 25 ml of distilled water and mixed thoroughly. The mixture was heated to 55^{o}C for 25 minutes stirring constantly to prevent local overheating.

2.9.2.5. Preparation of standard glucose solution

1 mM glucose was used as stock. 0.1 to 1.0 μg/ml glucose solution was prepared from this stock. A final volume of 2 ml was made with distilled water.

2.9.2.6. Determination of reducing sugar

Two ml of extract was taken in a test tube and 2 ml of solution III was added to it. Two ml of standard glucose solution was taken in another test tube and similarly, 2 ml of solution III was added to it. A blank with 2 ml of distilled water was also run.

Test tubes with samples were then boiled in long narrow tubes (to prevent oxidation) at 70^{o}C for 10 minutes. After boiling, the

tubes were quickly placed in ice-cold water. After that, 2 ml of arsenomolybdate was added rapidly to the test tubes and shaken well. The combined extract was made up to a final volume of 20 ml with distilled water.

Finally, absorbance of reducing sugar was measured at 520 nm wavelength with a spectrophotometer (Model SP6, UV/VIS PYE UNICUM, Japan).

The concentration of reducing sugar in the extract was calculated using a standard curve for reducing sugar (Fig. 9).

The amount of reducing sugar in the tissue was calculated using the following formula:

$$\text{Amount of reducing sugar} = \frac{\text{Concentration of sugar in the tissue} \times \text{Final volume of the extract} \times \text{Atomic weight of sugar} \times 1000}{\text{Fresh weight of the tissue} \times \text{Atomic weight of sugar} \times 1000}$$

2.9.3. Measurement of total sugar

Total sugar content was measured by the phenol-H_2SO_4 method (Dubois *et al.* 1956, Immers 1964).

In order to measure total sugar, 0.5 ml of extract was taken in a test tube and 0.5 ml of 5% aqueous phenol was added to it. 3 ml of concentrated H_2SO_4 was added rapidly direct into the solution in the test tube and mixed well. The tube was placed in cold water for 10 minutes.

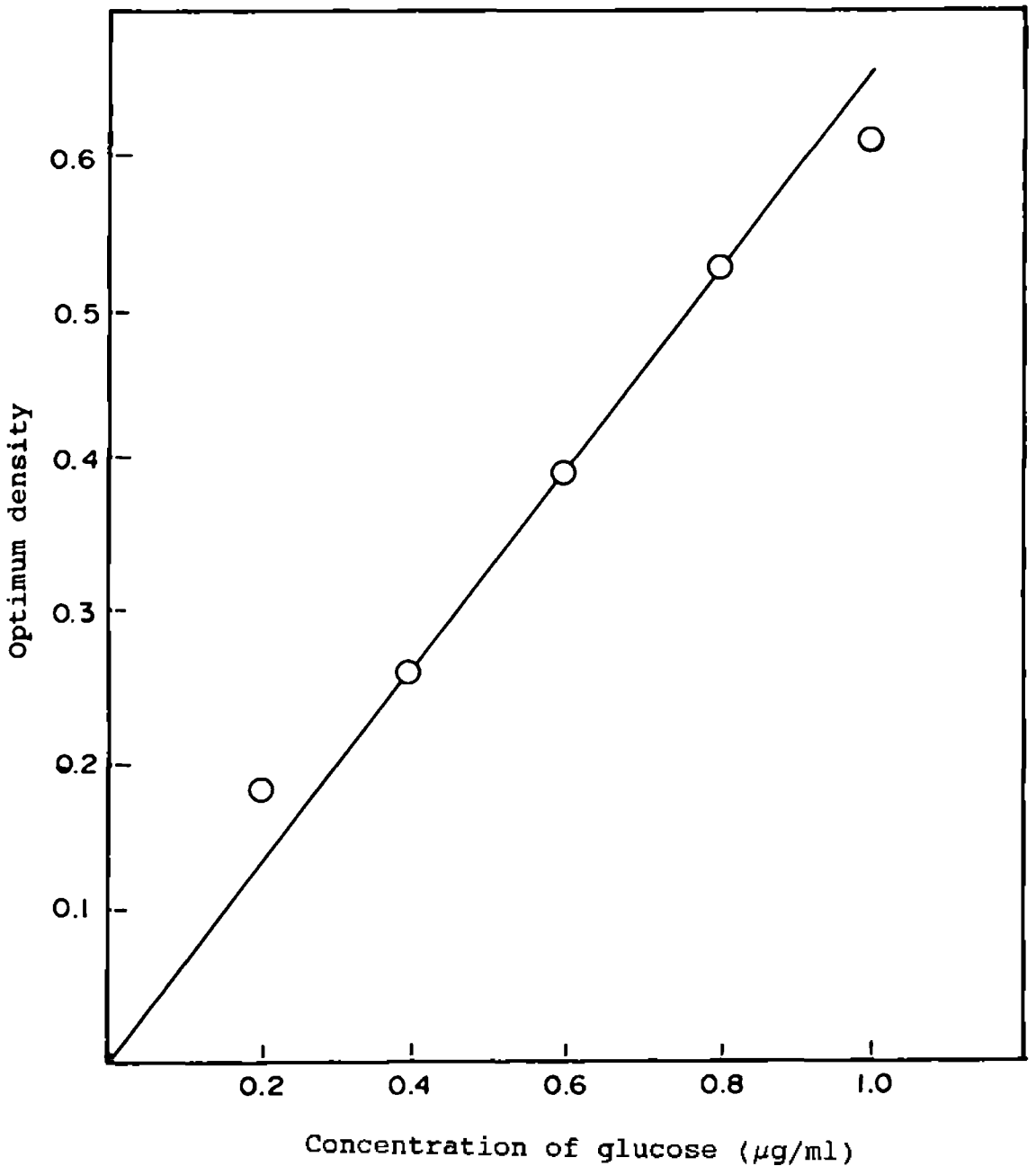

Fig. 9. Standard curve for reducing sugar

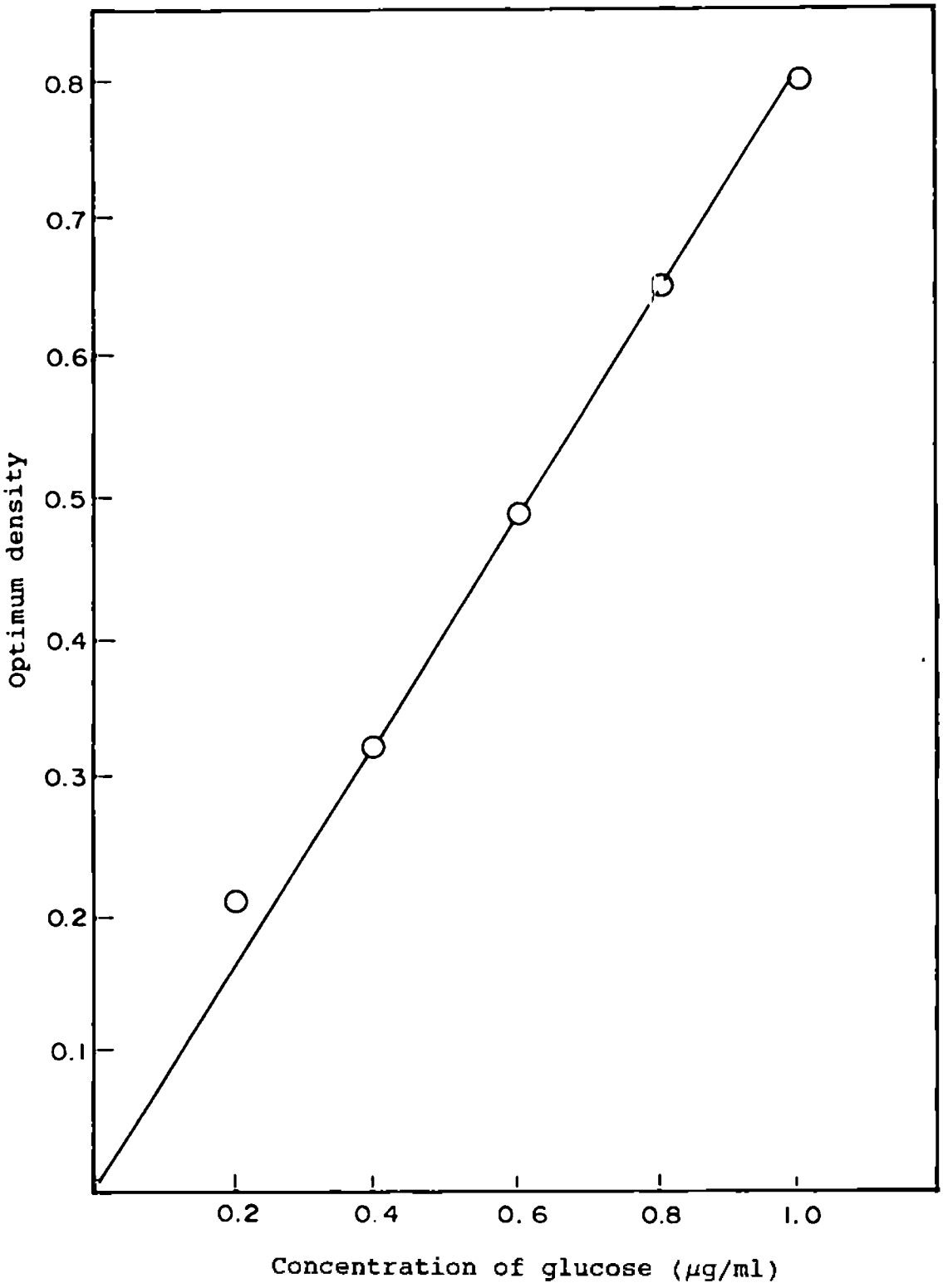

Fig. 10. Standard curve for total sugar

Finally, absorbance of total sugar was measured at 490 nm wavelength with a spectrophotometer (Model: Shimadzu Spectrophotometer UV-120-02, Japan).

The concentration of total sugar in the extract was calculated using a standard curve for total sugar (Fig. 10).

The amount of total sugar in the tissue was calculated using the following formula:

$$\text{Total sugar content} = \frac{\text{Concentration of sugar in the tissue} \times \text{Final volume of the extract} \times \text{Atomic weight of sugar} \times 1000}{\text{Fresh weight of the tissue} \times \text{Atomic weight of sugar} \times 1000}$$

CHAPTER 3

The effect of phytohormones on monovalent and divalent cations transport in excised root systems of rice seedlings

3.1. Introduction

The effect of phytohormones on ion transport in excised root systems were widely investigated (Van Steveninck 1976, Karmoker 1984). Indole acetic acid (IAA) stimulated K^+ and Na^+ uptake in pea internode segment (Lado *et al.* 1976). On the contrary, Zsoldos and Haunold (1982) showed that IAA inhibited K^+, NH_4^+ and NO_3^- uptake in rice root. Castro and Oliveira (1982) reported that IAA decreased Na^+, Ca^{2+} and Mg^{2+} content in the soybean stem. IAA-induced inhibition of PO_4^{2-} absorption was also found in excised plant tissue (Hourmant and Penot 1978a). α-naphthalene acetic acid (α-NAA) caused a greater increase in Cl^- uptake of coleoptile cells (Rubinstein 1973, Rubinstein and Light 1973).

Ion transport in excised root systems may be regulated by gibberellic acid (GA). As for example, Karmoker and Begum (1989) found that GA stimulated K^+ and Cl^- accumulation in the excised root systems of mungbean seedlings. GA_3 increased PO_4^{2-} uptake by 27% in foliar disc of *Pelargonium zonale* (Beraud and Penot 1988). On the contrary, Hourmant and Penot (1978b) found GA_3 induced decrease of PO_4^{2-} uptake in potato tuber discs.

The regulation of ion transport in excised root system may be very much affected by ABA. Van Stveninck (1972a) reported that ABA increased net uptake of K^+, Na^+ and Cl^- in beet root discs. ABA-induced inhibition of K^+ and Cl^- uptake was also found in *Avena* coleoptile sections (Reed and Bonner 1974). Dekock *et al.* (1978) reported that at low concentration ABA increased Ca^{2+} content but at high concentration, it caused a decrease of K^+, Ca^{2+} and P content in the fronds of *Lemna gibba*. ABA created a rapid influence on the content and reabsorption of K^+ and Ca^{2+} but did not show any significant effect on Mg^{2+} and Mn^{2+} in isolated *Cicer aerietinum* (Marlo and co-workers 1986). Palmer (1982) showed that ABA stimulated NO_3^- accumulation in fresh potato tubar slices.

A number of reports regarding the effect of kinetin on ion transport in excised tissues was published. Kinetin inhibited the transport of ions into the xylem of excised bean root systems (Karmoker 1982), into the xylem of sunflower root (Glinka 1980) and in barley root (Dieffenbach *et al.* 1980). On the contrary, Alamgir and Maximov (1983) reported that kinetin increased K^+ transport in the roots of corn seedlings. Karmoker and Razia (1993) reported that kinetin inhibited K^+ and Cl^- accumulation but stimulated Na^+ accumulation in excised roots of rice seedlings. On the other hand, kinetin caused a decrease in K^+ and Cl^- accumulation and also caused a decrease in Na^+ accumulation in excised root system of jute (Karmoker and Baten 1992). An initial increase of ^{45}Ca accumulation in *Amaranthus*

tricolor cotyledons was fond by cytokinin (Elliott and Yuguang 1989). Kinetin caused a decrease of inorganic phosphate absorption (Palmer 1976) and SO_4^{2-} absorption (Neirinckx 1968) whereas it increased Mg^{2+} accumulation in isolated lupine cotyledons (Przymusinski *et al.* 1981).

In this chapter, the effect of ABA and kinetin on the transport of monovalent and divalent cations in excised root systems of rice seedlings is reported.

3.2. Materials and Methods

3.2.1. Culture of plants

Plants were grown according to the methods described in 2.4.

3.2.2. Methods of ion transport experiment with excised root systems

Ion transport experiment with excised root systems was performed following the method described in 2.5.

Stock solution of ABA or kinetin was prepared according to method described in 2.3.4 or 2.3.5. ABA on kinetin was used at concentrations of 10^{-7}, 10^{-6} and 10^{-5} M.

3.2.3. Collection and drying of samples

Samples were collected and dried according to the method described in 2.7.

3.2.4. Methods of extraction of ions

The dried excised root systems were digested by acid mixture (concentrated $HClO_4$ at 4:1 ratio) according to the method described in 2.8.1.

3.2.5. Measurement of monovalent and divalent cations in excised root systems

Monovalent cations (K^+ and Na^+) were measured following the method described in 2.8.3.

Divalent cations (Ca^{2+}, Mg^{2+} and Fe^{2+}) were measured according to the method described in 2.8.4.

3.3. Results

3.3.1. The effect of ABA on the accumulation of monovalent cations in excised root systems of rice seedlings

In excised root tissue, 10^{-7} M ABA decreased K^+ accumulation by 11.0 to 27.6% at 3 to 6 hours of treatment. The inhibitory effect gradually declined and was levelled with the control at 24 and 48 hours of treatment (Fig. 11). At 10^{-6} M, ABA decreased the accumulation of K^+ by 21.7 to 16.8% at 3 to 48 hours of treatment (Fig. 11). ABA, at the concentration of 10^{-5} M, also caused a decrease in K^+ accumulation by 17.3 to 12.8% at 24 to 48 hours of treatment in excised root of rice seedlings (Fig. 11).

ABA (10^{-7} M) inhibited the accumulation of Na^+ by 34.1, 44.9, 33.2 and 20.0% at 3, 6, 24 and 48 hours of treatment respectively

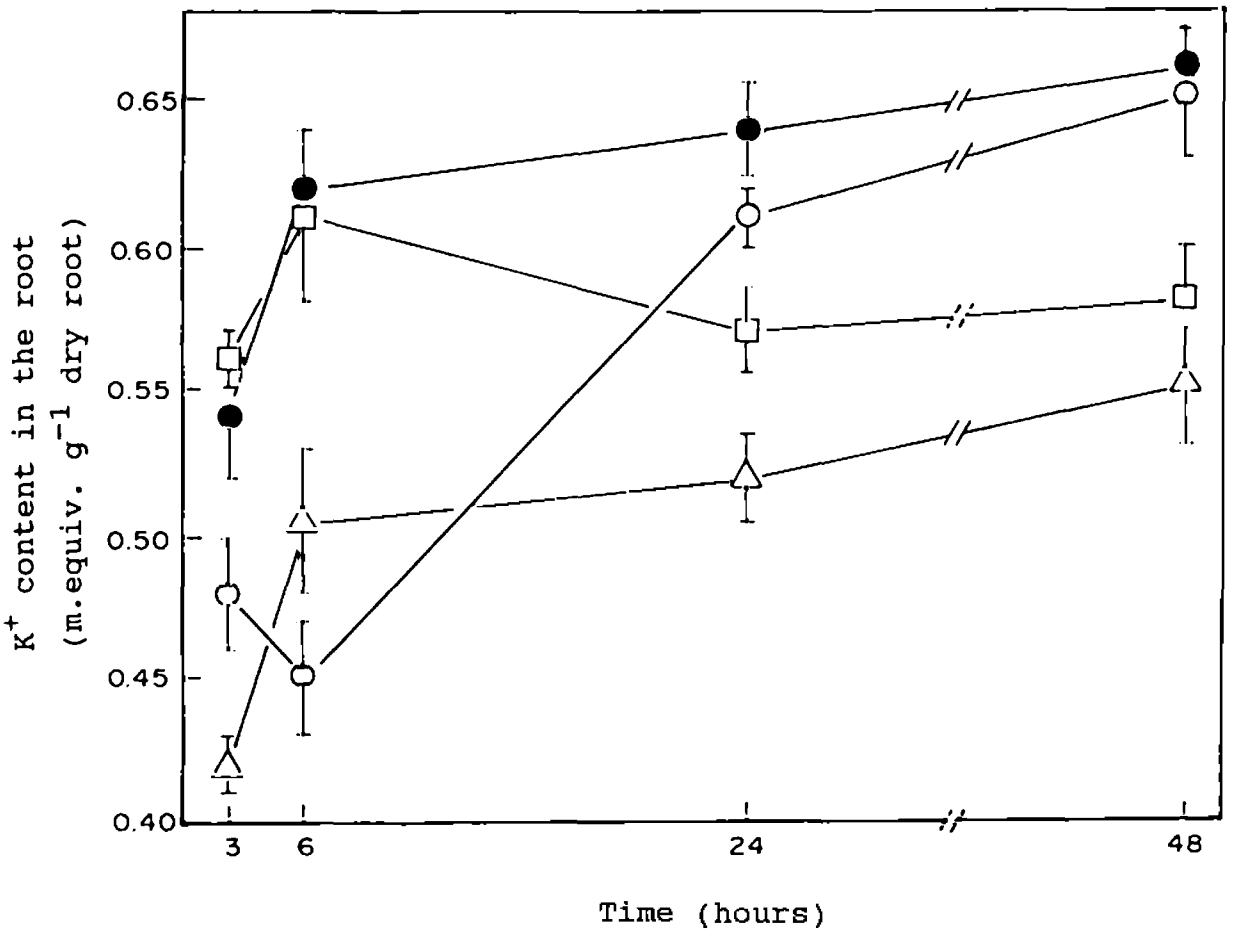

Fig. 11. The effect of different concentrations of ABA on K^+ accumulation in excised root systems of rice seedlings placed in half strength Hoagland solution with or without ABA. (●) represents control; (○) 10^{-7} M ABA; (△) 10^{-6} M ABA; (□) 10^{-5} M ABA. Each point represent the mean of three replicates; the bar represent ± standard error.

in excised root systems (Fig. 12). At 10^{-6} M ABA decreased Na^+ accumulation by 11.0 to 28.0% at 6 to 48 hours of treatment (Fig. 12). At the concentration of 10^{-5} M, ABA caused an inhibition of Na^+ accumulation by 33.7 to 25.4% at 3 to 48 hours of treatment in excised roots of rice seedlings (Fig. 12).

3.3.2. The effect of ABA on the accumulation of divalent cations in excised root systems of rice seedlings

In excised root tissue, 10^{-7} M ABA inhibited Ca^{2+} accumulation by 12.1, 20.3 and 14.2% at 3, 6 and 24 hours of treatment respectively (Fig. 13). Similarly, ABA, at 10^{-6} M, caused an inhibition of Ca^{2+} accumulation by 9.1, 6.7 and 8.8% at 3, 6 and 24 hours of treatment respectively (Fig. 13). At the concentration of 10^{-5} M, ABA also inhibited Ca^{2+} accumulation by 8.1 to 5.6% at 6 to 48 hours of treatment after an initial increase at 3 hours of treatment (Fig. 13).

ABA (10^{-7} M) did not show any significant effect on Mg^{2+} accumulation in excised root tissue (Fig. 14). At the concentration of 10^{-6} M, ABA decreased Mg^{2+} accumulation by 14.7 to 16.7% at 24 to 48 hours of treatment (Fig. 14). Similarly, 10^{-5} M ABA decreased Mg^{2+} accumulation by 20.1 to 20.6% at 24 to 48 hours of treatment in excised root of rice seedlings (Fig. 14).

ABA, at 10^{-7}, 10^{-6} and 10^{-5} M, decreased Fe^{2+} accumulation at 6 to 24 hours of treatment after an initial promotion at 3 hours of treatment in excised root systems. The inhibitory effect

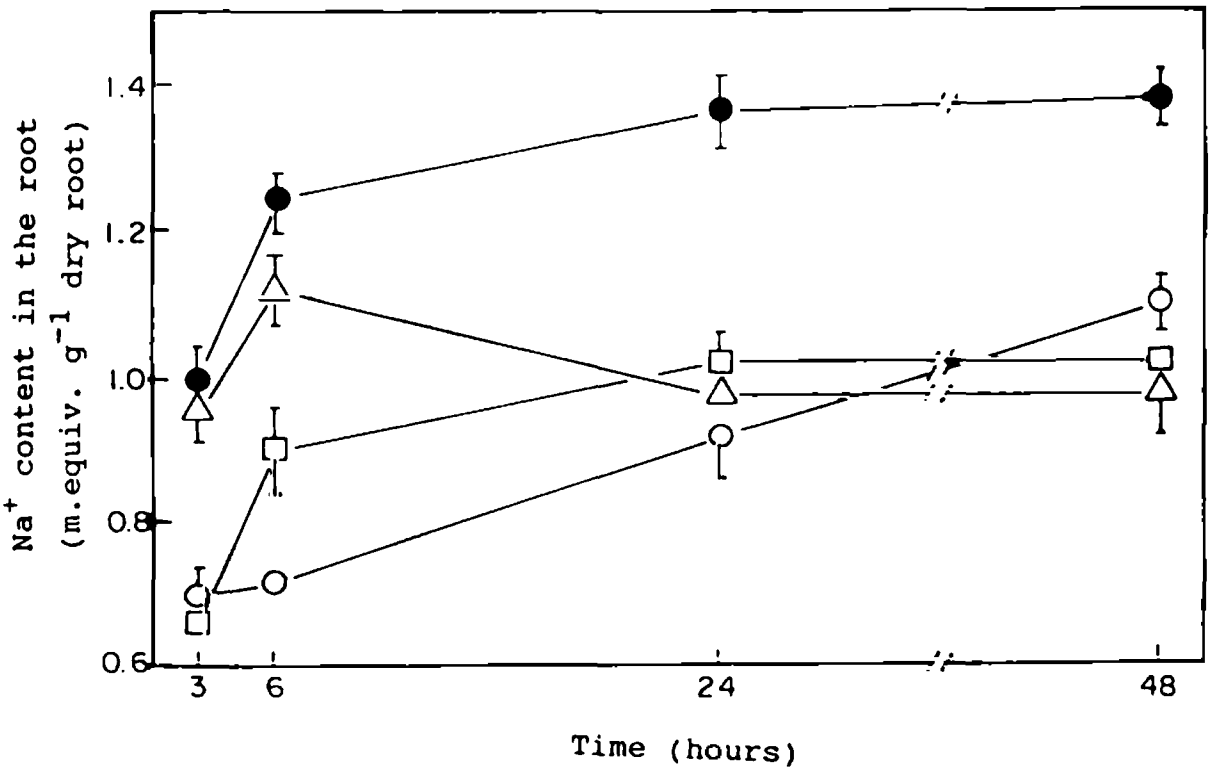

Fig. 12. The effect of different concentrations of ABA on Na^+ accumulation in excised root systems of rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

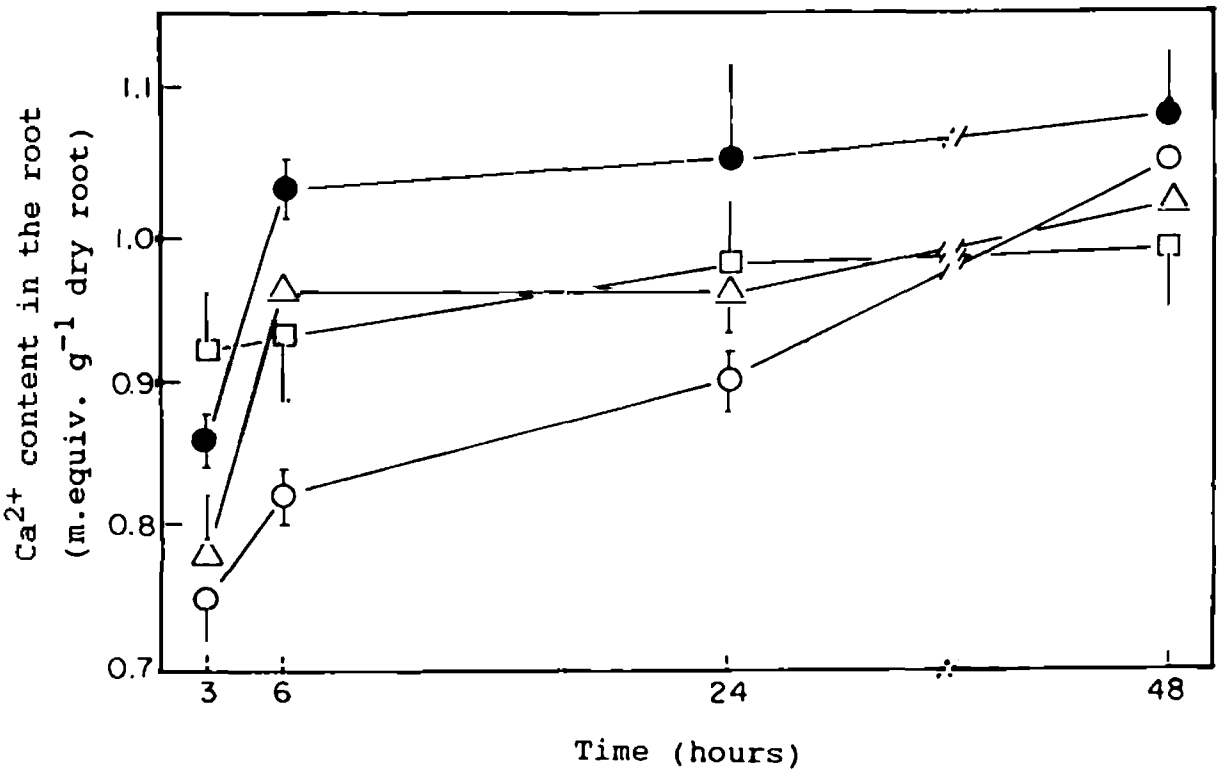

Fig. 13. The effect of different concentrations of ABA on Ca^{2+} accumulation in excised root systems of rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

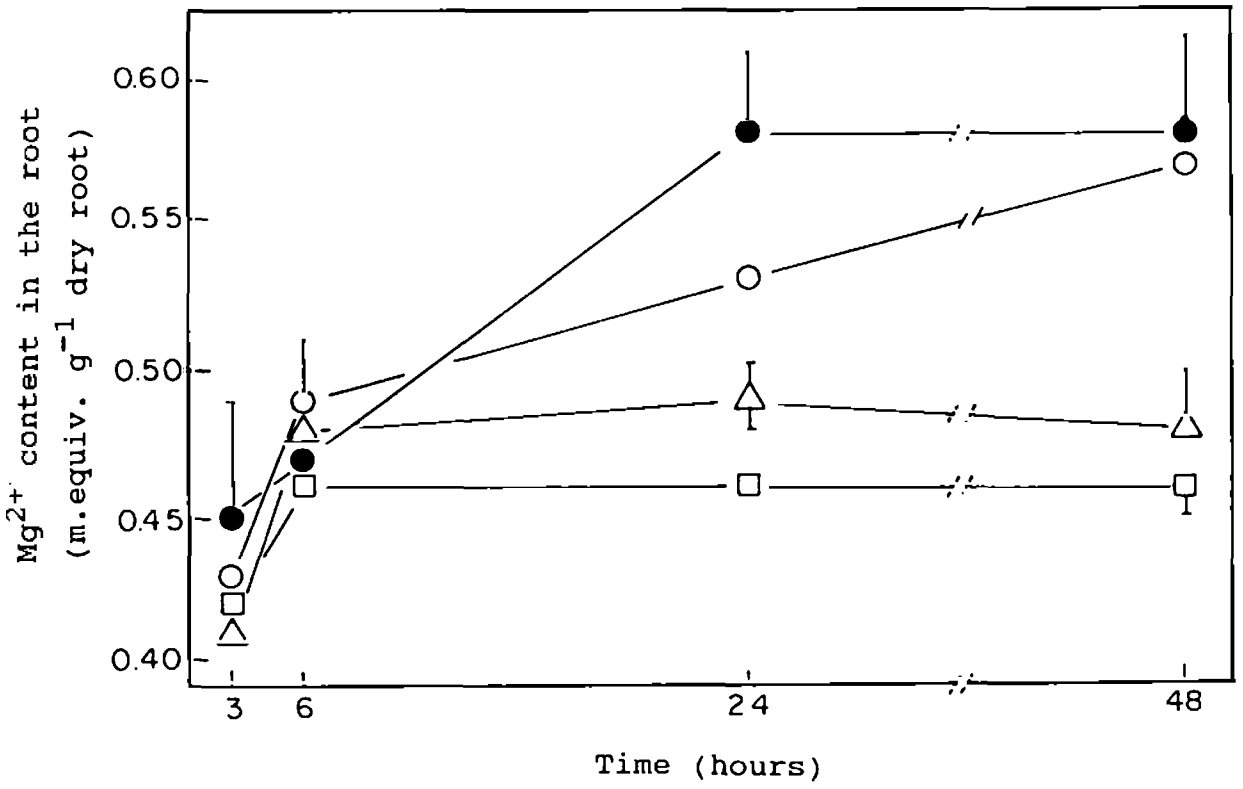

Fig. 14. The effect of different concentrations of ABA on Mg^{2+} accumulation in excised root systems of rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

gradually declined after 24 hours of treatment leading to a stimulation at 48 hours of treatment (Fig. 15). Maximum inhibition was 22.9% caused by 10^{-6} M ABA at 24 hours of treatment (Fig. 15).

3.3.3. The effect of kinetin on the accumulation of monovalent cations in excised root systems of rice seedlings

In excised root tissue, 10^{-7} and 10^{-6} M kinetin did not show any significant effect on K^+ accumulation (Fig. 16). At the concentration of 10^{-5} M, kinetin caused an inhibition of K^+ accumulation by 44.3 to 35.0% at 3 to 48 hours of treatment (Fig. 16).

Kinetin (10^{-7} M) caused an inhibition of Na^+ accumulation by 43.7 to 37.6% over a period of 3 to 48 hours of treatment in excised root systems (Fig. 17). Similarly, 10^{-6} M kinetin inhibited Na^+ accumulation by 9.2 to 15.9% at 3 to 48 hours of treatment (Fig. 17). At the concentration of 10^{-5} M, kinetin also inhibited Na^+ accumulation by 52.5 to 49.3% at 3 to 48 hours of treatment in excised root systems (Fig. 17).

3.3.4. The effect of kinetin on the accumulation of divalent cations in excised root systems of rice seedlings

In excised root, 10^{-7} M kinetin did not show any significant effect on Ca^{2+} accumulation (Fig. 18). At the concentration of 10^{-6} and 10^{-5} M, kinetin increased Ca^{2+} accumulation by 9.4 and 18.4% respectively at 24 hours of treatment and the accumulation

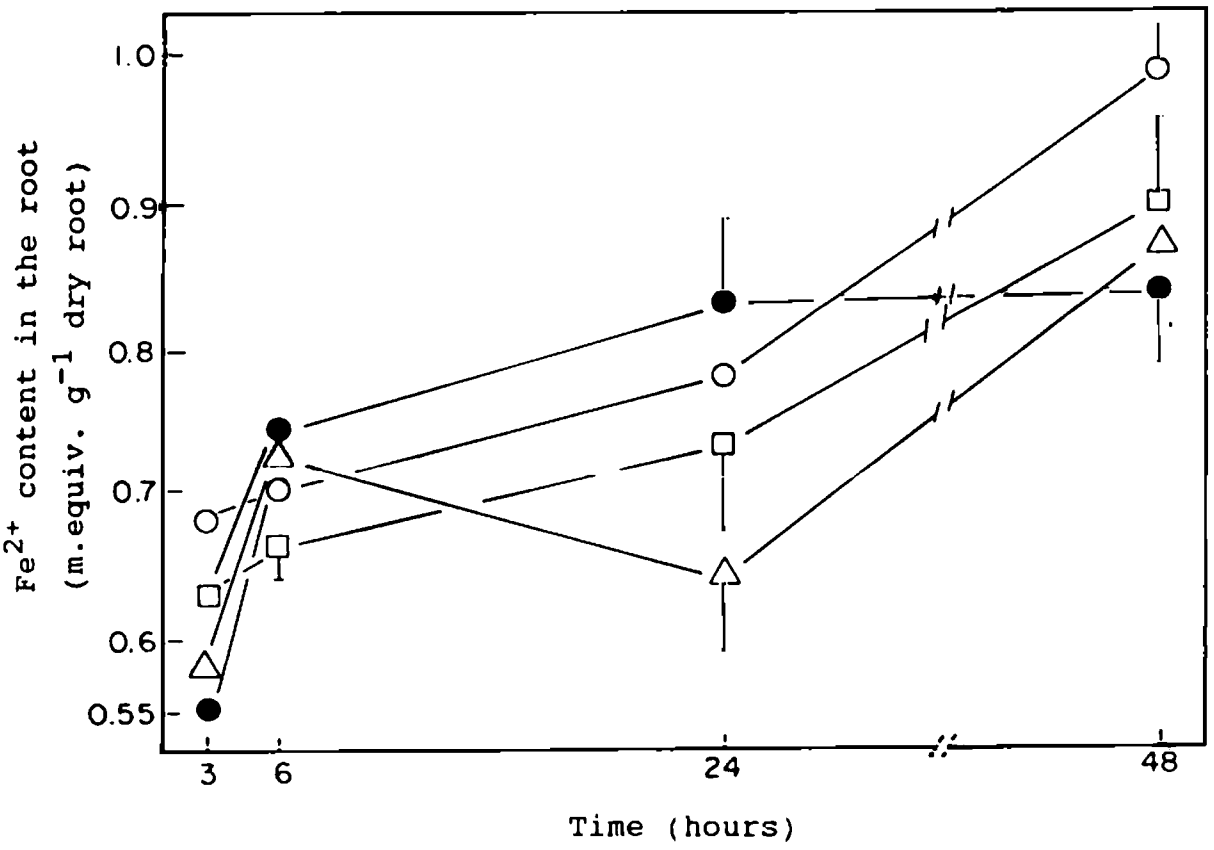

Fig. 15. The effect of different concentrations of ABA on Fe^{2+} accumulation in excised root systems of rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

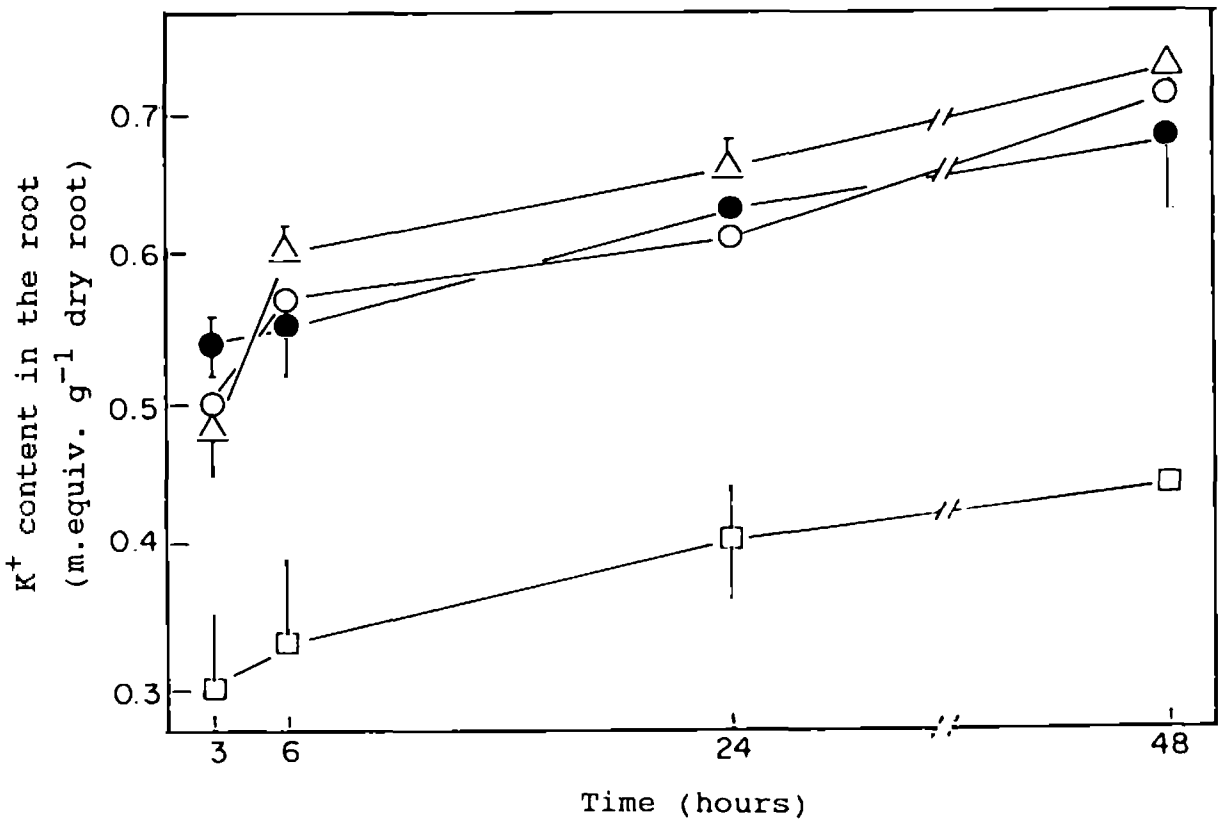

Fig. 16. The effect of different concentrations of kinetin on K^+ accumulation in excised root systems of rice seedlings placed in half strength Hoagland solution with or without kinetin. (●) represents control; (○) 10^{-7} M kinetin; (△) 10^{-6} M kinetin; (□) 10^{-5} M kinetin. Each point represent the mean of three replicates; the bar represent ± standard error.

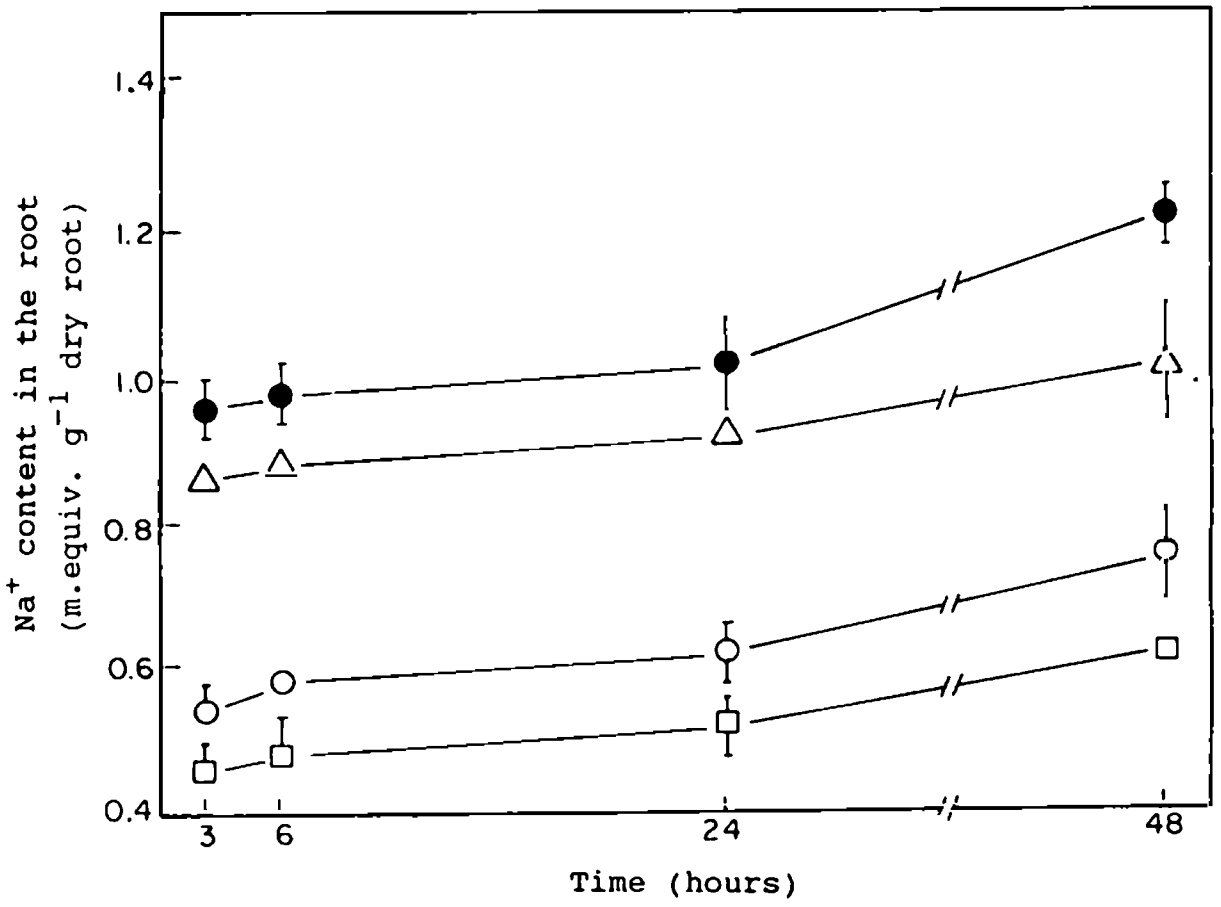

Fig. 17. The effect of different concentrations of kinetin on Na^+ accumulation in excised root systems of rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

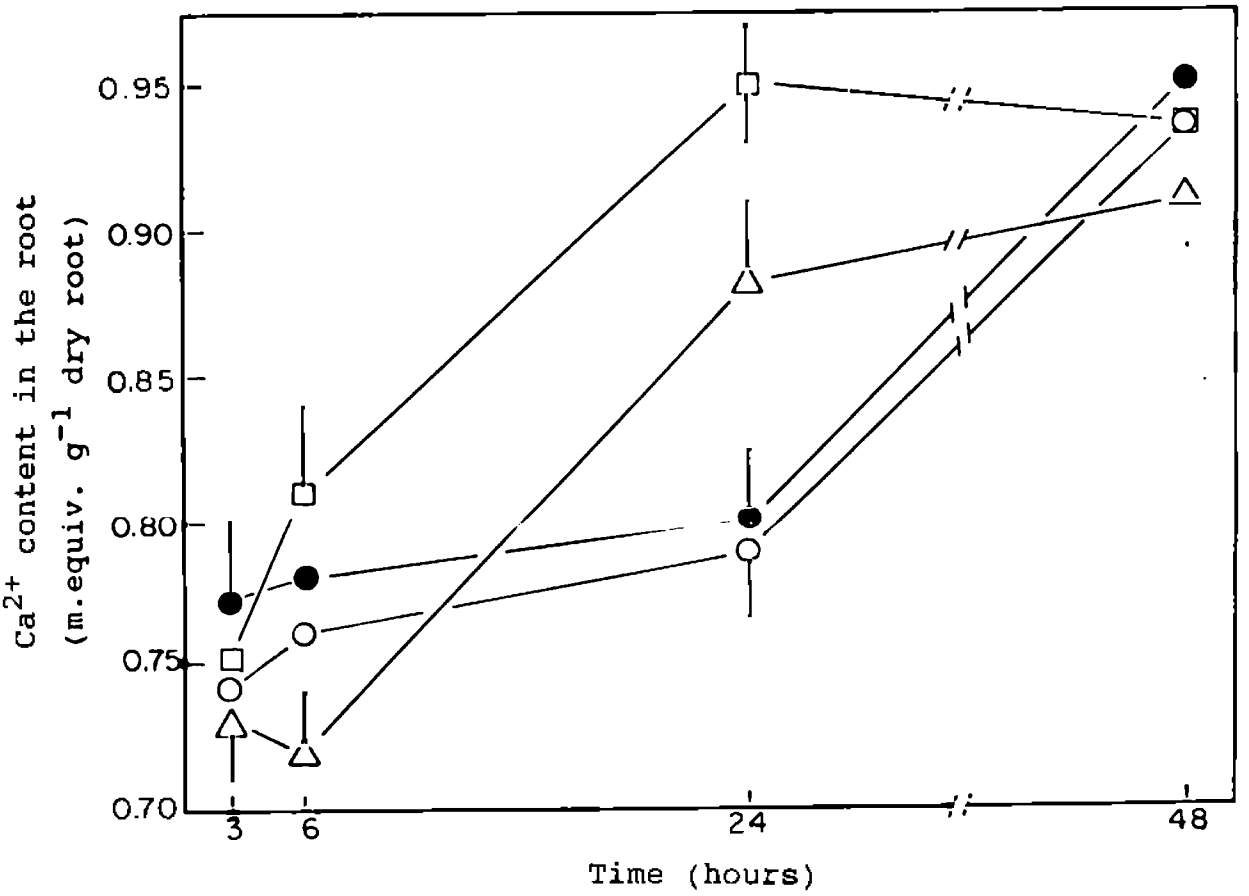

Fig. 18. The effect of different concentrations of kinetin on Ca^{2+} accumulation in excised root systems of rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

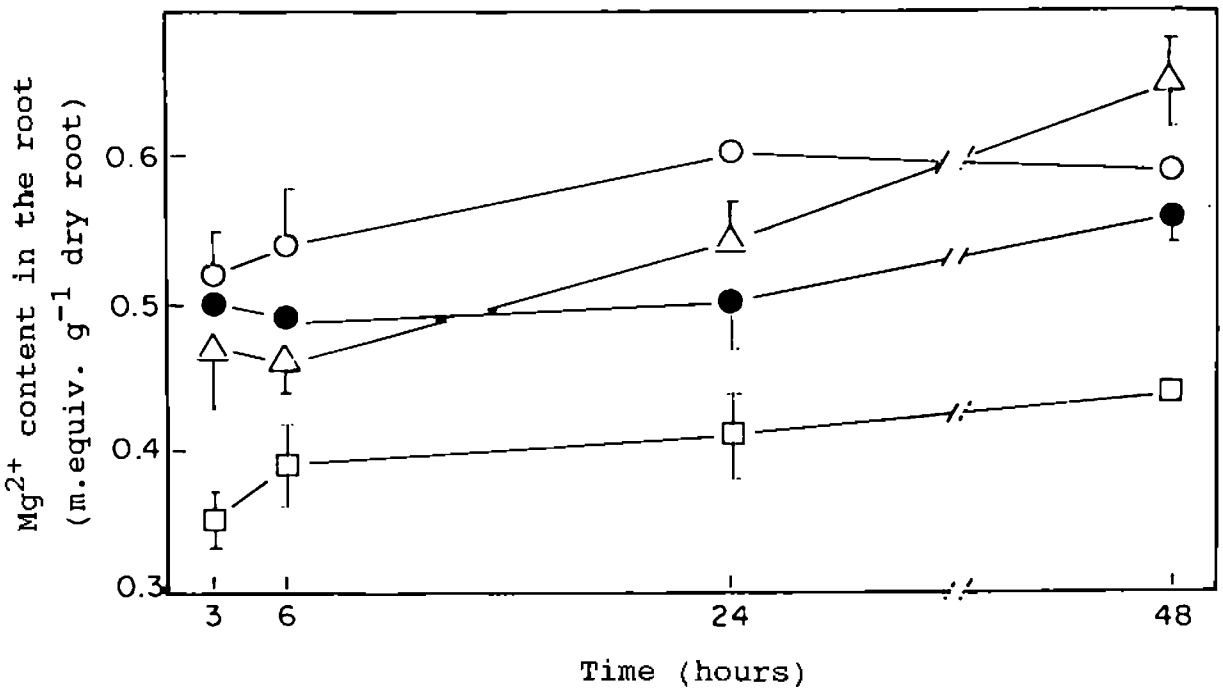

Fig. 19. The effect of different concentrations of kinetin on Mg^{2+} accumulation in excised root systems of rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

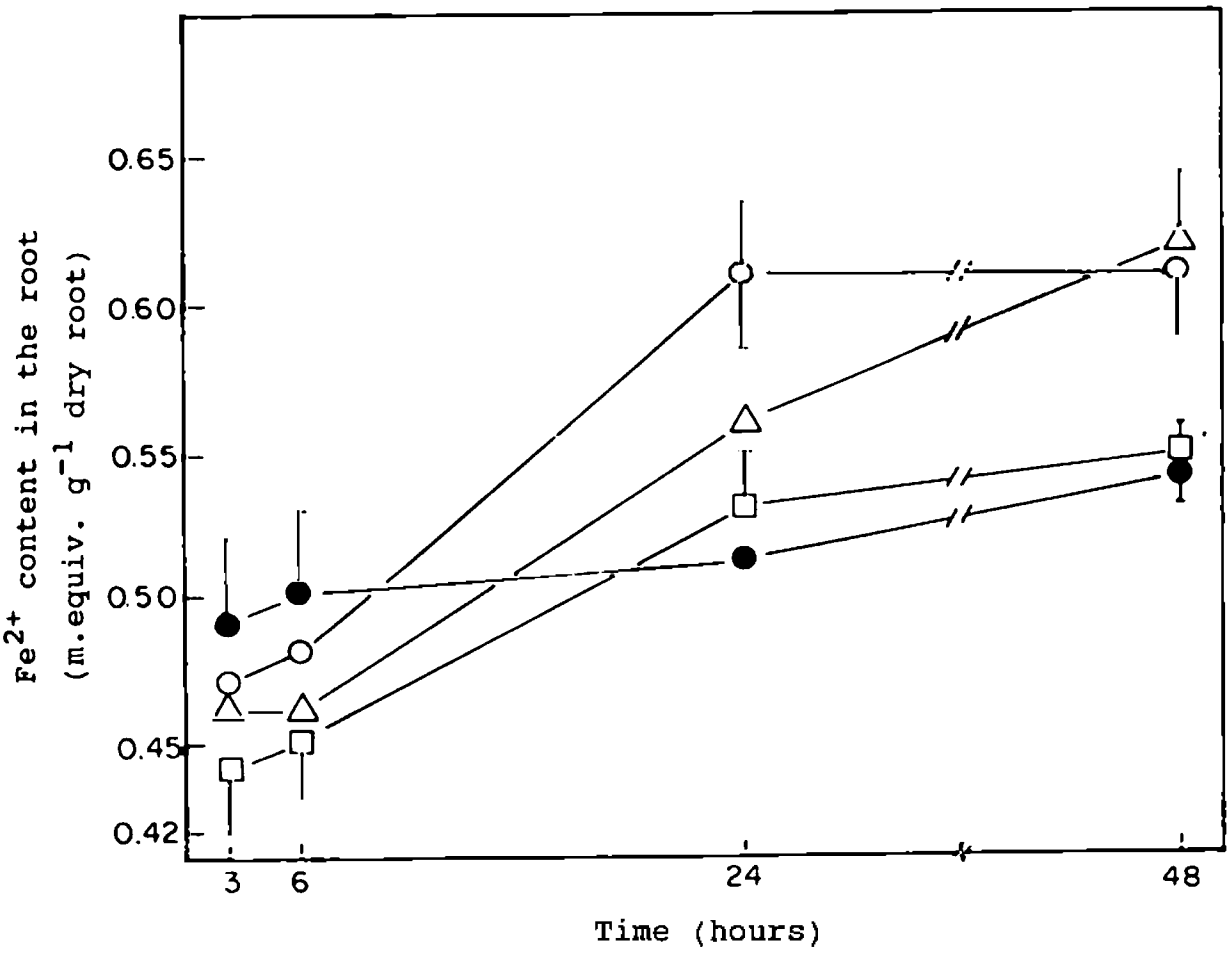

Fig. 20. The effect of different concentrations of kinetin on Fe^{2+} accumulation in excised root systems of rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

was almost levelled with the control at 48 hours of treatment (Fig. 18).

In excised root of rice seedlings, 10^{-7} M kinetin caused an increase in Mg^{2+} accumulation by 11.9, 18.6 and 11.7% at 6, 24 and 48 hours of treatment respectively (Fig. 19). 10^{-6} M kinetin also increased Mg^{2+} accumulation by 7.5 to 23.0% at 24 to 48 hours of treatment (Fig. 19). On the contrary, 10^{-5} M kinetin inhibited Mg^{2+} accumulation by 30.2 to 16.4% at 3-48 hours of treatment (Fig. 19).

Kinetin increased Fe^{2+} accumulation at 24-48 hours of treatment after an initial decrease at 3-6 hours of treatment in excised root systems of rice seedlings (Fig. 20). At the concentration of 10^{-7} and 10^{-6} M, kinetin increased Fe^{2+} accumulation by 18.4 to 12.7% and 8.1 to 14.3% respectively (Fig. 20).

3.4. Discussion

Abscisic acid (ABA) decreased both K^+ and Na^+ accumulation in excised root systems of rice seedlings (Fig. 11 and 12). This result is supported by the work of Behl and Jeschke (1979) who found that ABA decreased K^+ and Na^+ accumulation by 93 to 98% in excised barley roots. This is also supported by Cram and Pitman (1972) and Shanner and co-workers (1975) who found an inhibition of K^+ accumulation by ABA in excised barley roots and maize roots respectively. The inhibitory effect of ABA on K^+ and Na^+ accumulation may be due to a number of reasons. It may be due to the closing of stomata by the activity of ABA which was related

to ion transport (Mittelheuser and Van Staveninck 1969, 1971, Cummins *et al.* 1971, Kriedemann *et al.* 1972). ABA closed stomata with a concomitant inhibition of K^+ influx into guard cells (Mansfield and Jones 1971, Horton and Moran 1972). ABA-induced inhibition of K^+ and Na^+ transport (Fig. 11 and 12) may be due to ABA-induced inhibition of protein synthesis (Mothes *et al.* 1961) which are related with the regulation of ion transport (Van Steveninck 1976, Karmoker 1984).

ABA inhibited Ca^{2+} accumulation in excised root systems of rice seedlings (Fig. 13). This result is supported by the work of Dekock *et al.* (1978) who found that at high concentration (1 to 10 ppm), ABA decreased Ca^{2+} content in the fronds of *Lemna gibba*. The inhibitory effect of ABA on Ca^{2+} accumulation was also found in excised barley roots (Pitman and Wellfare 1978).

ABA decreased Mg^{2+} accumulation in excised root systems of rice seedlings (Fig. 14). The inhibitory effect of ABA on Mg^{2+} accumulation is supported by Pitman and Wellfare (1978) who found a ABA-incuded decrease of Mg^{2+} accumulation in excised barley roots.

ABA inhibited Fe^{2+} accumulation in excised root of rice seedlings (Fig. 15). The inhibitory effect of ABA on Fe^{2+} accumulation led to decrease in respiration.

Kinetin (10^{-5} M) inhibited K^+ accumulation over a period of 3 to 48 hours of treatment in excised root of rice seedlings (Fig. 16). Na^+ accumulation was also inhibited by kinetin

(Fig. 17). Similar inhibition of K^+ and Na^+ was recorded in excised jute root systems (Karmoker and Baten 1992). The inhibitory effect of kinetin on K^+ and Na^+ accumulation was also supported by Van Steveninck (1972b) who showed that kinetin inhibited net accumulation of K^+ and Na^+ in aged beet root tissue. Kinetin-induced inhibitory effect on ion transport was recorded in excised root systems of barley (Dieffenbach *et al.* 1980).

Kinetin (10^{-6} and 10^{-5} M) increased Ca^{2+} accumulation at 24 hours of treatment in excised rice root systems (Fig. 18). The stimulatory effect of kinetin on Ca^{2+} accumulation was also found in the protoplast of *Amaranthus tricolor* cotyledons (Elliott and Yuguang 1989).

Kinetin (10^{-7} and 10^{-6} M) increased Mg^{2+} accumulation in excised root of rice seedlings (Fig. 19). The stimulation of Mg^{2+} accumulation by kinetin may be due to kinetin-induced stimulation of ATPase activity with Mg^{2+} ions (Pryzymunsinski *et al.* 1981).

Kinetin increased Fe^{2+} accumulation after an initial decrease in excised root systems of rice seedlings (Fig. 20). The stimulatory effect of kinetin on Fe^{2+} accumulation led to increase in respiration.

CHAPTER 4

The effect of phytohormones on monovalent and divalent cations transport in intact rice seedlings

4.1. Introduction

Reports regarding the effect of phytohormones on ion transport in intact plants are comparatively less than excised tissue. The inhibitory effect of auxin on ion transport in intact bean plants (Castro and Oliveira 1982) and intact wheat plants (Swenson and Burström 1960) was reported. Votrubova and Votruba (1986) reported that the uptake of monovalent cations was promptly affected by IAA than divalent cations in intact maize seedlings.

GA stimulated Rb^+ transport in the shoot of intact sunflower (Benlloch *et al.* 1983) and Na^+ content in mungbean leaves but had no effect on K^+ transport (Karmoker and Begum 1989). Garcia and Guardiola (1981) reported that the uptake of Ca^{2+}, Mg^{2+} and K^+ in *Pisum sativum* cv Progress was stimulated by GA_3.

Karmoker and Van Steveninck (1978) reported that ABA caused a stimulation of Na^+ accumulation but caused an inhibition of K^+ accumulation in intact bean roots. Similar result was found in intact wheat seedlings (Gunvor and co-workers 1990). On the contrary, ABA was found to stimulate K^+ transport in intact root of *Hordeum vulgare* (Reidell and Schimid 1984).

Kinetin was also found to regulate the ion transport in intact plants. Kinetin decreased the uptake of K^+ and Ca^{2+} in the root of intact radish seedlings (Bittner and Buschmann 1983). On the contrary, Karmoker and Baten (1992) showed that kinetin increased the accumulation of K^+ and Na^+ in the roots of intact jute seedlings. Net influx and long distance transport of those ions was also increased by kinetin.

In this chapter, the effect of ABA and kinetin on the transport of monovalent and divalent cations in intact rice seedlings are reported.

4.2. Materials and Methods

4.2.1. Culture of plants

Plants were grown according to the methods described in 2.4.

4.2.2. Methods of ion transport experiment with intact seedlings

Ion transport experiment with intact seedlings was performed following the method described in 2.6.

Stock solution of ABA or kinetin was prepared as described in 2.3.4 and 2.3.5. ABA or kinetin was used at the concentration of 10^{-7}, 10^{-6} and 10^{-5} M.

4.2.3. Collection and drying of samples

Samples were collected and dried according to the method described in 2.7.

4.2.4. Methods of extraction of ions

Ions were extracted following the method described in 2.8.1.

4.2.5. Measurement of monovalent and divalent cations in intact seedlings

Monovalent cations (K^+ and Na^+) was measured following the method described in 2.8.3.

Divalent cations (Ca^{2+}, Mg^{2+} and Fe^{2+}) was measured according to the method described in 2.8.4.

4.3. Results

4.3.1. The effect of ABA on the accumulation of monovalent cations in intact seedlings

In intact root of rice seedlings, 10^{-7} M ABA decreased K^+ accumulation by 26.2 to 8.0% at 6 to 48 hours of treatment after an initial increase of 21% at 3 hours of treatment (Fig. 21a). Similarly, 10^{-6} M ABA caused an initial 9% increase followed by a decrease by 18.1 to 10.3% at 6 to 48 hours of treatment (Fig. 21a). ABA, at the concentration of 10^{-5} M, also caused a decrease in K^+ accumulation by 9.0 to 17.4% at 6 to 48 hours of

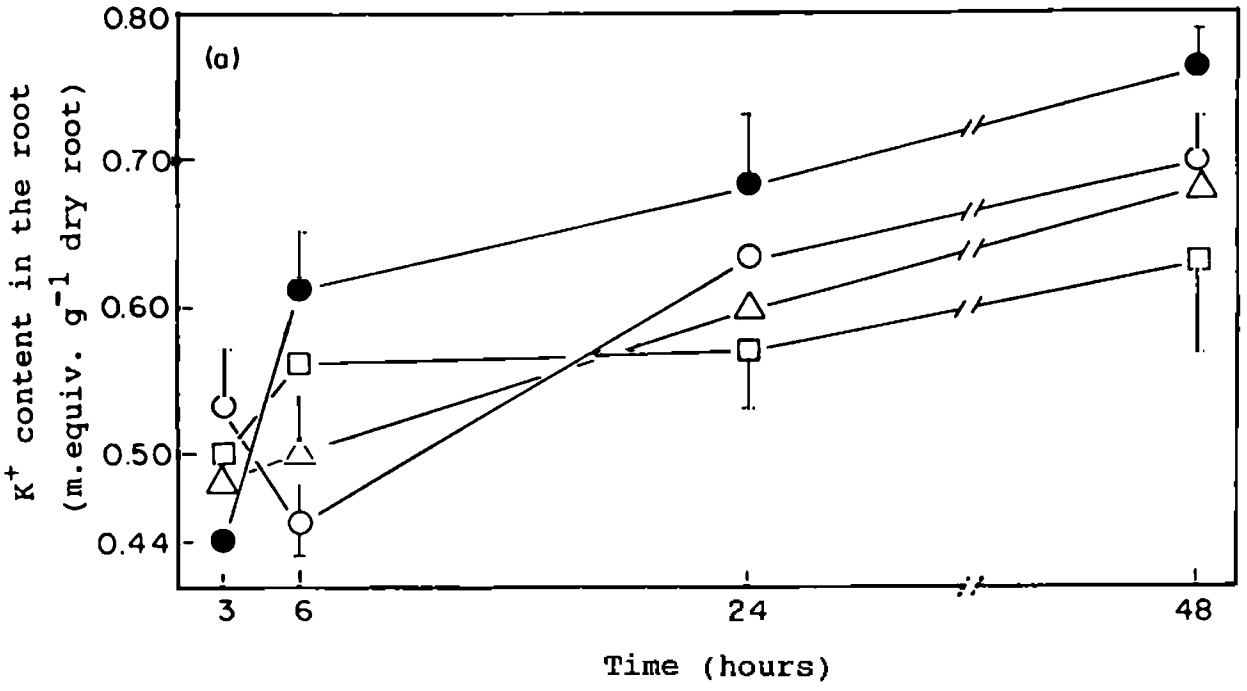

Fig. 21a. The effect of different concentrations of ABA on K^+ accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

treatment after an initial increase by 13% at 3 hours of treatment (Fig. 21a).

In the shoot of intact rice seedlings, 10^{-7} M ABA inhibited K^+ accumulation by 10.8 to 16.1% at 6 to 48 hours of treatment (Fig. 21b). 10^{-6} M ABA also caused a decrease in K^+ accumulation by 9.0 to 7.0% at 3 to 48 hours of treatment in the shoot of intact seedlings (Fig. 21b). Similarly, 10^{-5} M ABA inhibited K^+ accumulation by 17.3 to 9.0% at 6 to 48 hours of treatment (Fig. 21b).

In the root of intact rice seedlings, 10^{-7} M ABA did not show any significant effect on Na^+ accumulation (Fig. 22a). At the concentration of 10^{-6} M, ABA decreased Na^+ accumulation by 7.0% at 3 to 24 hours of treatment and then gradually levelled with the control within 48 hours of treatment (Fig. 22a). On the other hand, 10^{-5} M ABA inhibited Na^+ accumulation by 6.5 to 9.3% at 3 to 24 hours of treatment (Fig. 22a).

In the shoot of intact seedlings, 10^{-7} M ABA caused a decrease in Na^+ accumulation by 10.0, 11.0 and 10.7% at 3, 6 and 48 hours of treatment respectively (Fig. 22b). At the concentration of 10^{-6} M, ABA decreased Na^+ accumulation by 10.0% at 48 hours of treatment (Fig. 22b). On the other hand, 10^{-5} M ABA did not show any significant effect on Na^+ accumulation (Fig. 22b).

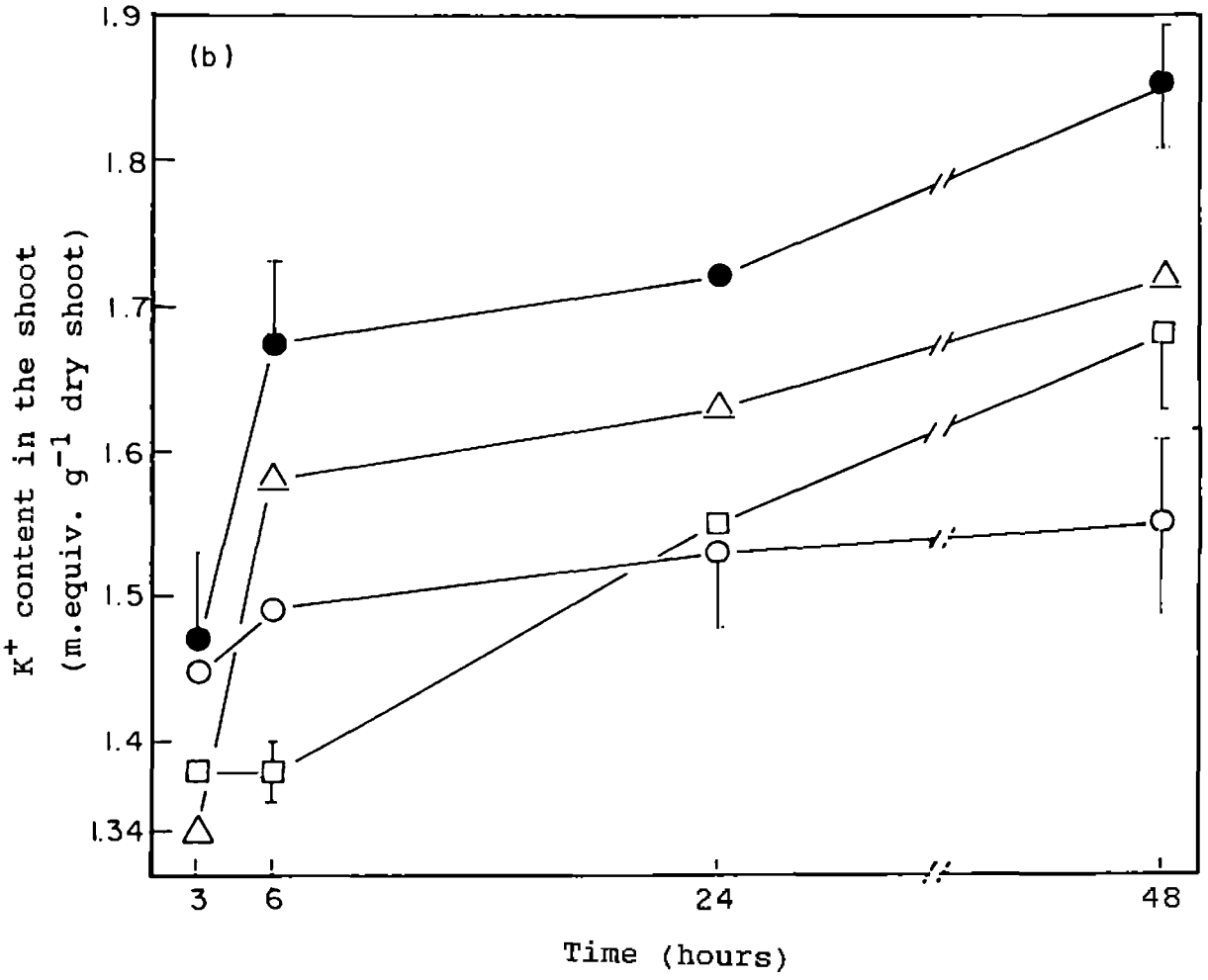

Fig. 21b. The effect of different concentrations of ABA on K^+ accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

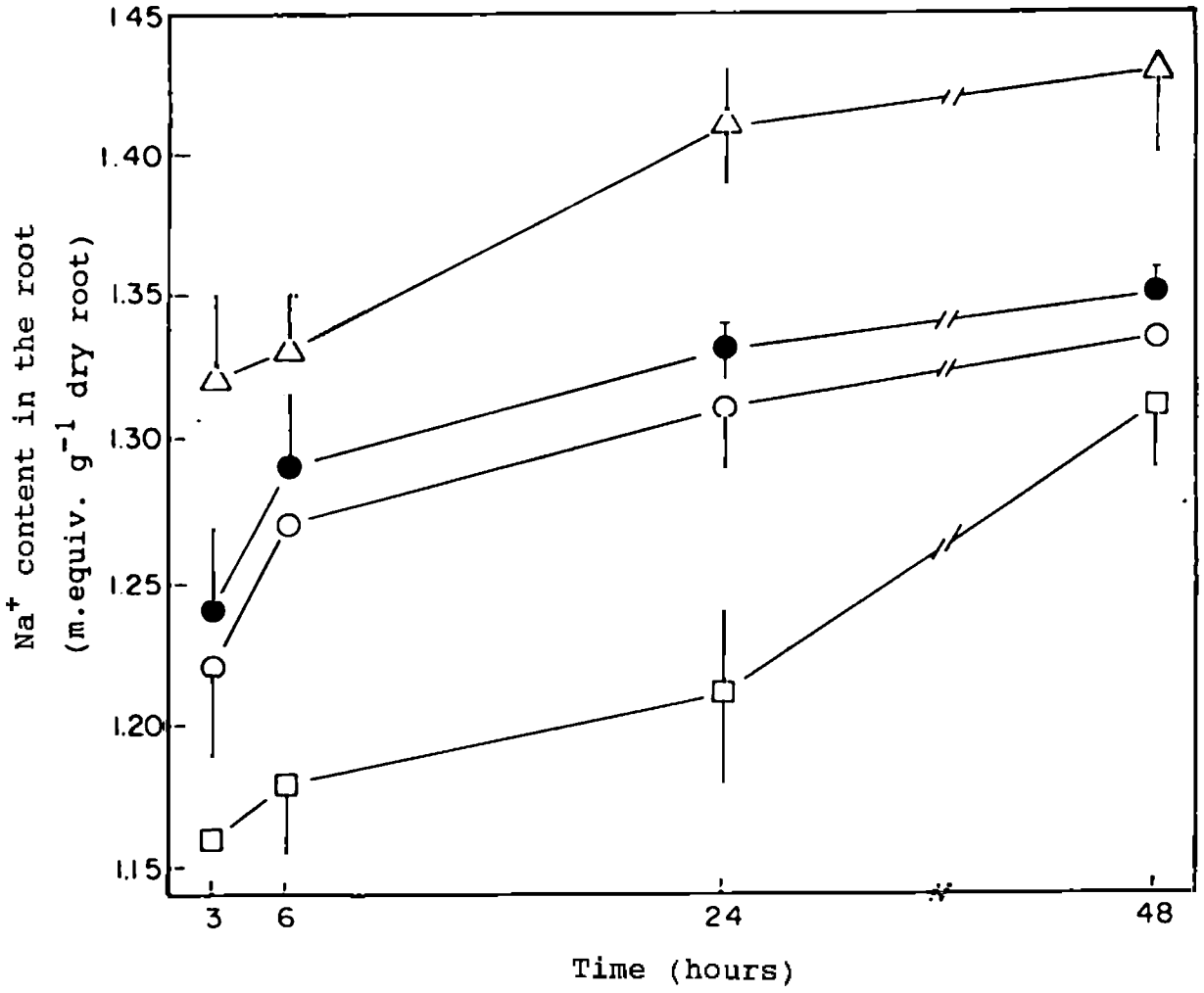

Fig. 22a. The effect of different concentrations of ABA on Na^+ accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

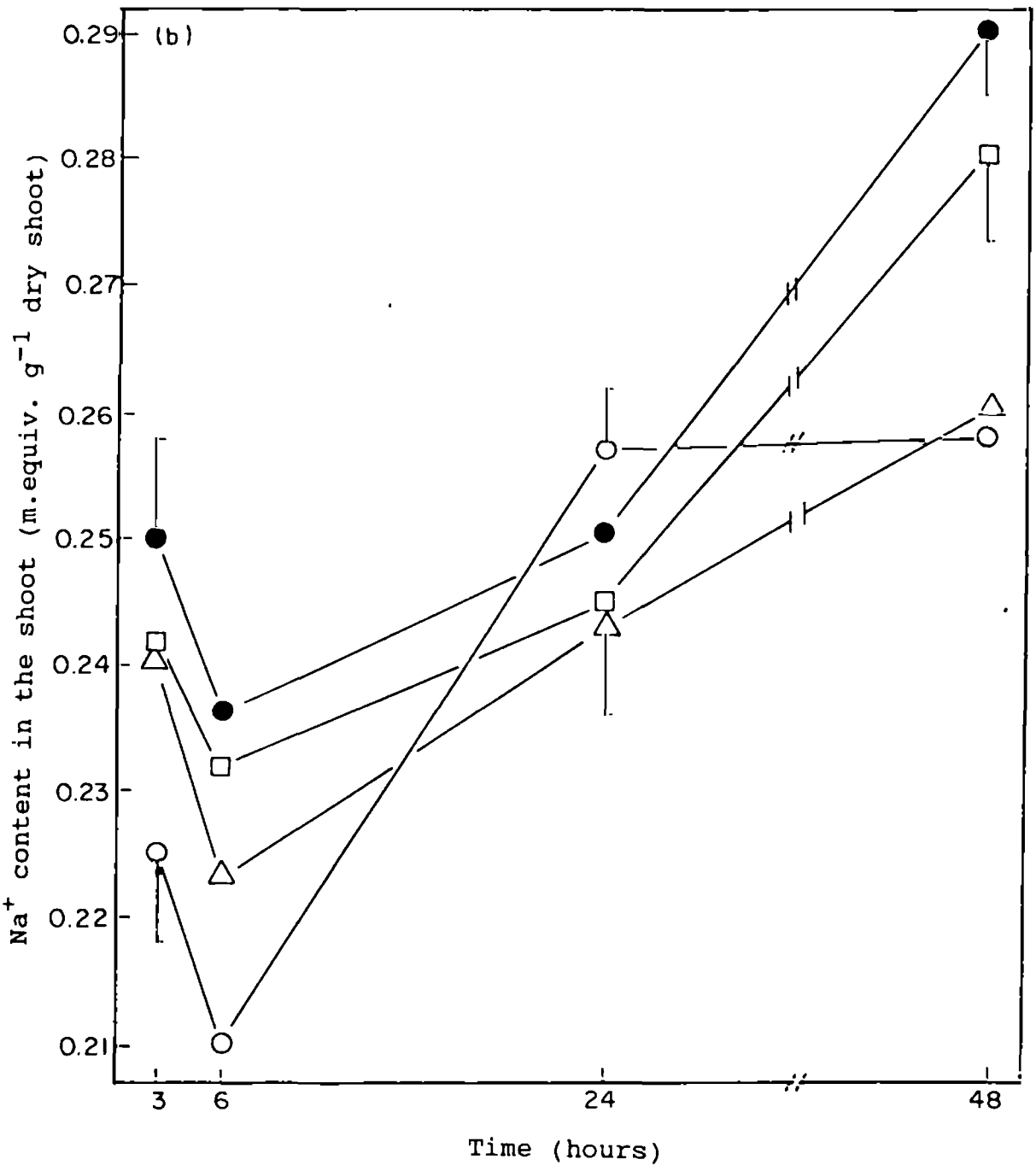

Fig. 22b. The effect of different concentrations of ABA on Na^+ accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

4.3.2. The effect of ABA on the accumulation of divalent cations in intact rice seedlings

In the root of intact rice seedlings, 10^{-7} M ABA increased Ca^{2+} accumulation by 21.4% at 6 hours of treatment and the stimulatory effect was maintained up to 48 hours of treatment (Fig. 23a). At the concentration of 10^{-6} M, ABA caused an increase in Ca^{2+} accumulation by 15.2% at 6 hours of treatment and gradually levelled with the control within 48 hours of treatment (Fig. 23a). ABA, at 10^{-5} M, caused a stimulation of Ca^{2+} accumulation by 43.5 to 26.7% at 6 to 48 hours of treatment after an initial decrease at 3 hours of treatment (Fig. 23a).

In the shoot of intact rice seedlings, 10^{-7} M ABA caused a gradual decrease in Ca^{2+} accumulation by 8.2 to 13.0% at 6 to 48 hours of treatment after an initial increase by 11.8% at 3 hours of treatment (Fig. 23b). 10^{-6} M ABA stimulated Ca^{2+} accumulation by 25.4, 9.2 and 21.7% at 3, 6 and 48 hours of treatment respectively (Fig. 23b). ABA, at 10^{-5} M, also caused a stimulation of Ca^{2+} accumulation by 35.8% at 6 hours of treatment which was then levelled with the control within 48 hours of treatment (Fig. 23b).

In the root of intact rice seedlings, 10^{-7} M ABA increased Mg^{2+} accumulation by 36.2, 39.6 and 13.1% at 6, 24 and 48 hours of treatment respectively after an initial decrease by 13.4% at 3 hours of treatment (Fig. 24a). 10^{-6} M ABA also increased Mg^{2+} accumulation by 8.3 to 25.7% at 3 to 48 hours of treatment (Fig. 24a). At the concentration of 10^{-5} M, ABA caused a

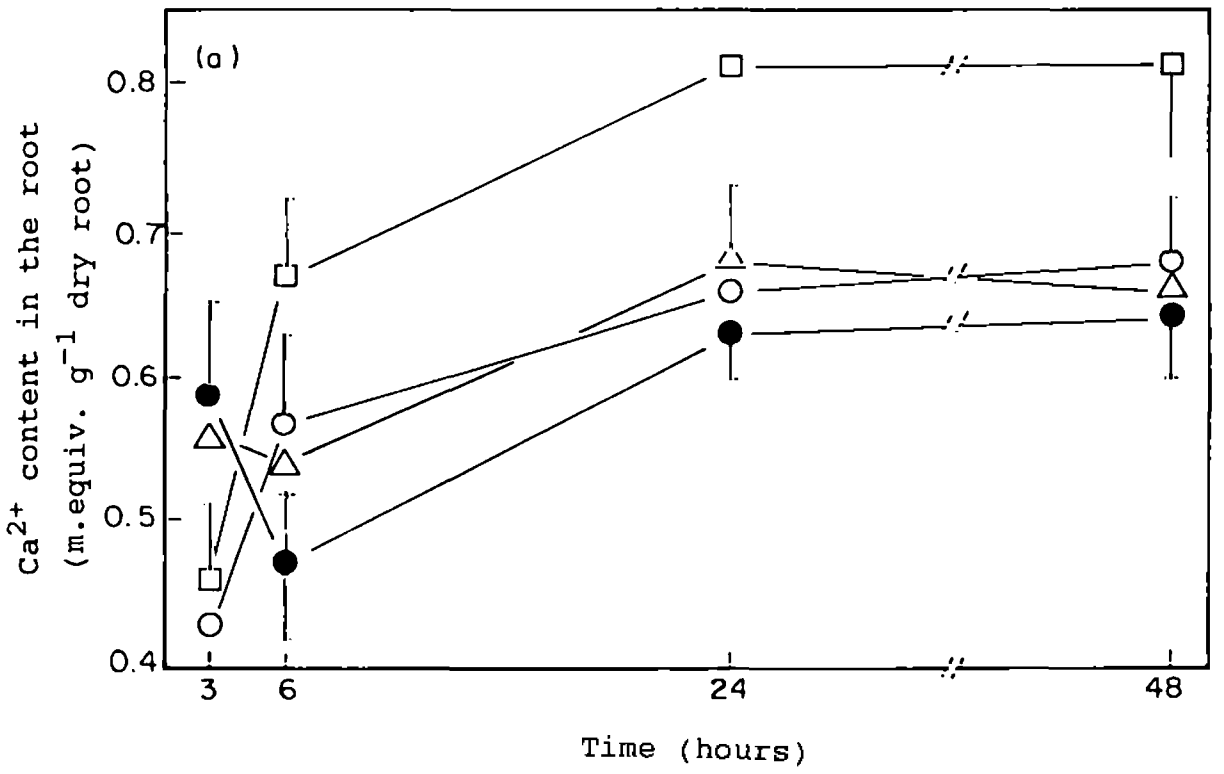

Fig. 23a. The effect of different concentrations of ABA on Ca^{2+} accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

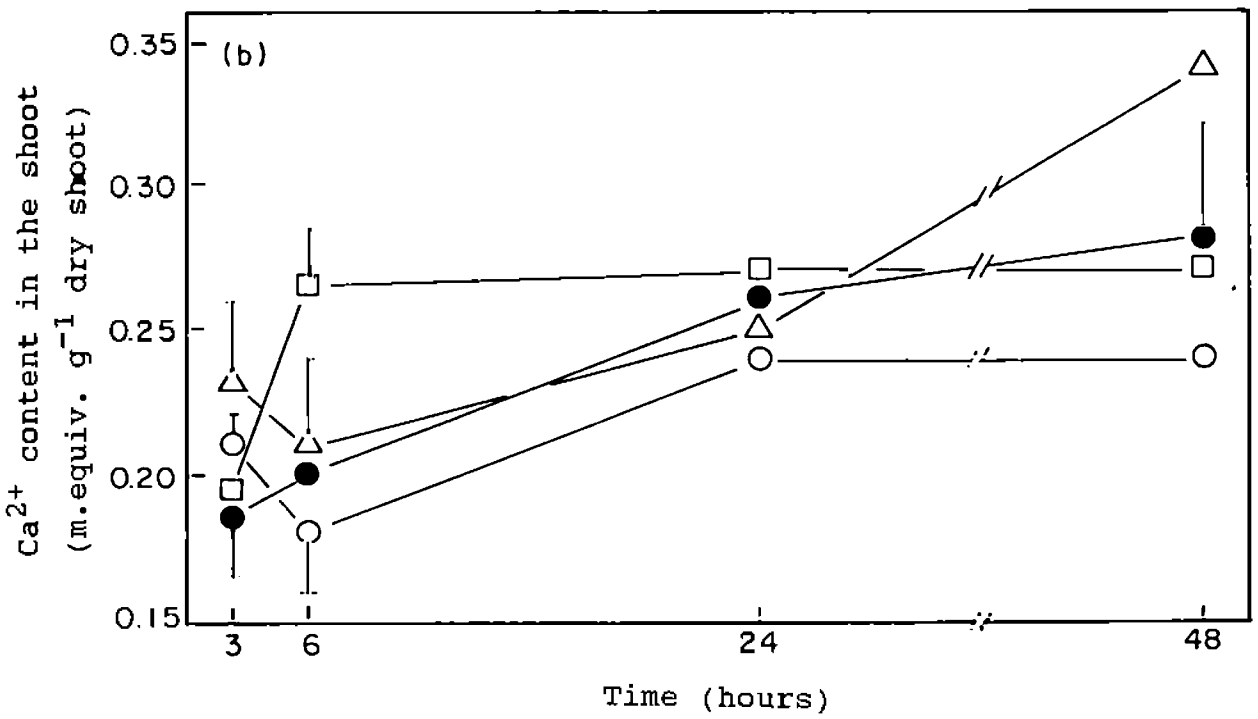

Fig. 23b. The effect of different concentrations of ABA on Ca^{2+} accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

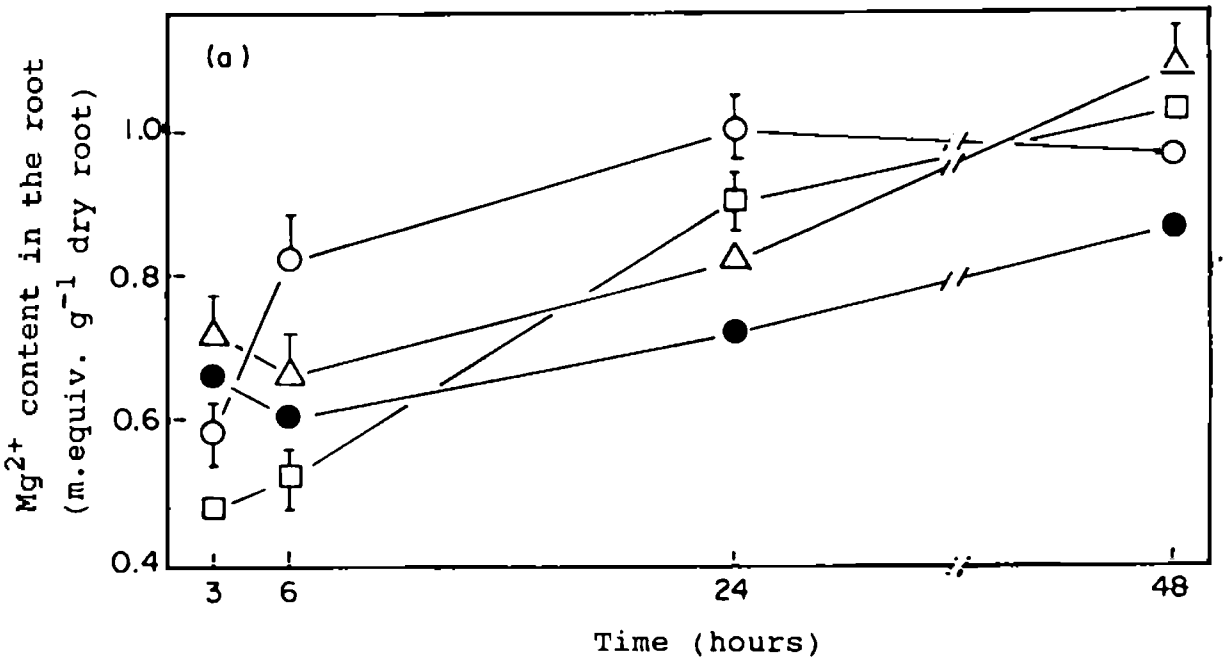

Fig. 24a. The effect of different concentrations of ABA on Mg^{2+} accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

decrease in Mg^{2+} accumulation by 28.0 to 14.4% at 3 to 6 hours of treatment followed by an increase by 24.3 to 19.7% at 24 to 48 hours of treatment in the root of intact seedlings (Fig. 24a).

In the shoot of intact rice seedlings, 10^{-7} M ABA did not show any significant effect on Mg^{2+} accumulation up to 48 hours of treatment (Fig. 24b). 10^{-6} M ABA increased Mg^{2+} accumulation by 8.0 to 10.0% at 6 to 24 hours of treatment after an initial inhibition at 3 hours of treatment (Fig. 24b). At the concentration of 10^{-5} M, ABA caused a decrease in Mg^{2+} accumulation by 12.8, 16.7 and 8.8% at 3, 24 and 48 hours of treatment respectively in the shoot of intact seedlings (Fig. 24b).

In the root of intact rice seedlings, 10^{-7} M ABA caused an inhibition in Fe^{2+} accumulation by 34.9, 28.0 and 12.2% at 6, 24 and 48 hours of treatment respectively (Fig. 25a). ABA, at 10^{-6} M, also inhibited Fe^{2+} accumulation by 37.9% at 6 hours of treatment. The inhibitory effect was maintained up to 48 hours of treatment (Fig. 25a). At the concentration of 10^{-5} M, ABA caused an inhibition in Fe^{2+} accumulation by 53.8 to 10.1% at 6 to 48 hours of treatment after an initial increase by 9.2% at 3 hours of treatment in the root of intact seedlings (Fig. 25a).

In the shoot of intact rice seedlings, 10^{-7} M ABA increased Fe^{2+} accumulation by 26.0 to 15.0% at 3 to 6 hours of treatment followed by a decreased by 16.4 to 11.4% at 24 to 48 hours of treatment (Fig. 25b). Similarly, 10^{-6} M ABA increased Fe^{2+} accumulation by 35.7 to 20.0% at 3 hours of treatment followed by

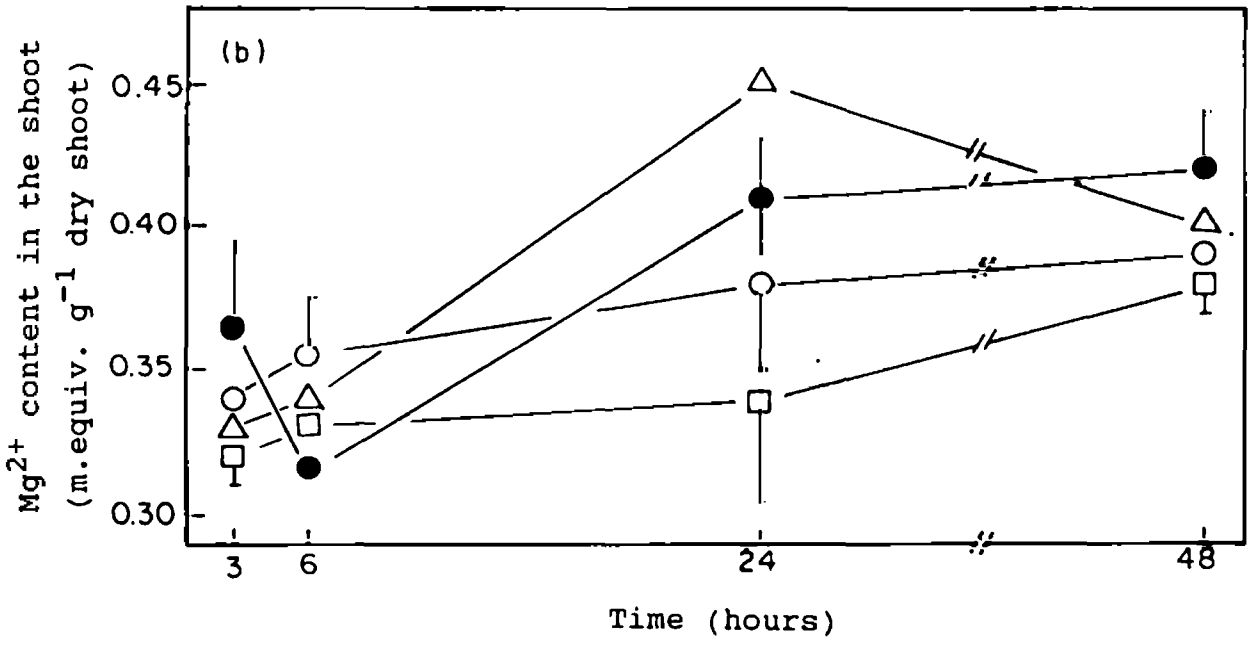

Fig. 24b. The effect of different concentrations of ABA on Mg^{2+} accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

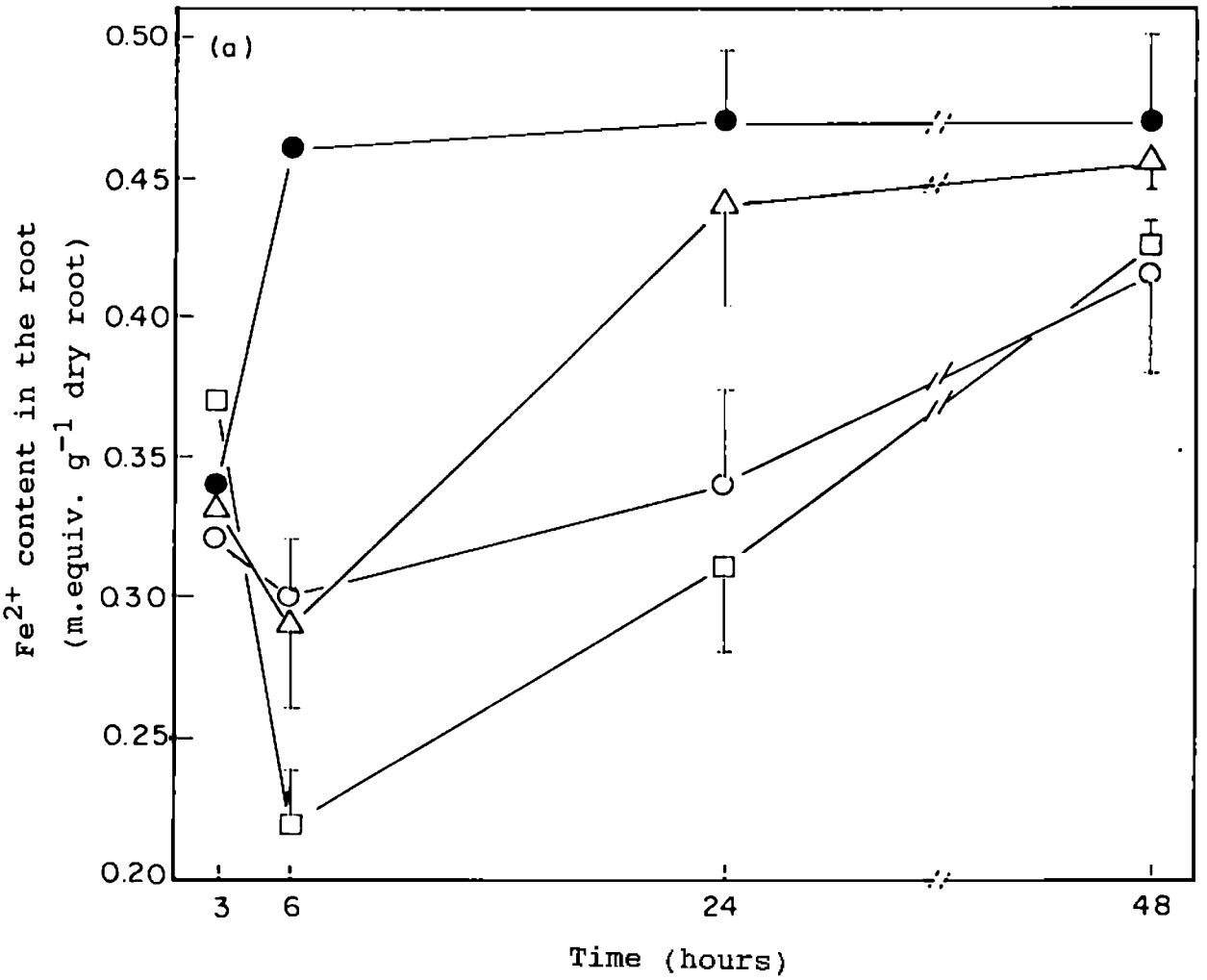

Fig. 25a. The effect of different concentrations of ABA on Fe^{2+} accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

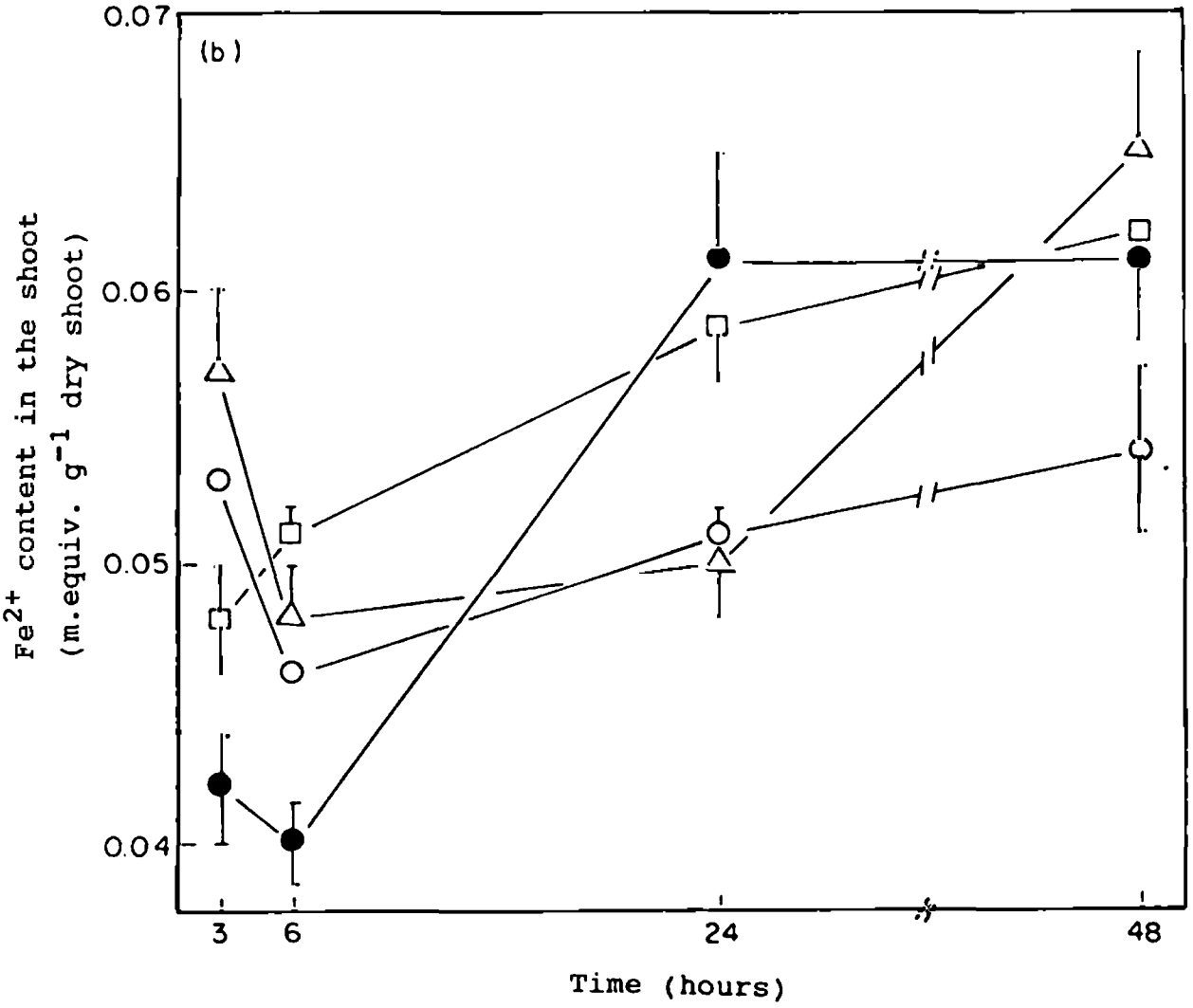

Fig. 25b. The effect of different concentrations of ABA on Fe^{2+} accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

a decrease by 18.0% at 24 hours of treatment (Fig. 25b). At the concentration of 10^{-5} M, ABA increased Fe^{2+} accumulation by 14.2 to 27.5% at 3 to 6 hours of treatment in the shoot of intact seedlings. The inhibitory effect was nullified at 24 to 48 hours of treatment (Fig. 25b).

4.3.3. The effect of ABA on net influx and long distance transport of monovalent cations in intact rice seedlings

In intact rice seedlings, 10^{-7} M ABA decreased net influx (Ψ_{oc}) of K^+ by 19.7% at 24 hours of treatment (Table 2). ABA, at 10^{-6} M, also decreased net influx of K^+ by 13.3% at 24 hours of treatment (Table 2). The net influx of K^+ in intact seedlings increased by 25.9 and 13.9% at following ABA (10^{-5} M) treatment at 6 and 48 hours respectively (Table 2).

ABA (10^{-7} M) inhibited long distance transport (Ψ_{cx}) of K^+ by 25.1% at 24 hours of treatment (Table 2). Similarly, 10^{-6} M ABA inhibited long distance transport of K^+ by 13.3% at 24 hours of treatment (Table 2). ABA, at 10^{-5} M, also inhibited long distance transport of K^+ by 27.3 and 12.3% at 6 and 24 hours of treatment respectively in intact rice seedlings (Table 2).

ABA (10^{-7} M) increased transport index of K^+ at 6 hours of treatment but decreased that at 3 and 24 hours of treatment (Table 2). 10^{-6} M ABA increased transport index of K^+ at 3 to 6 hours of treatment but did not show any significant effect at 24 to 48 hours of treatment (Table 2). At 10^{-5} M, ABA decreased

Table 2. The effect of ABA on net influx and long distance transport of K^+ in intact rice seedlings placed in half strength Hoagland solution with or without ABA. Each value is the mean of three replicates; ± represents standard error.

Time (hr)	Transport of K^+ from root to shoot (γ_{cx}) (mg/shoot)				Net influx of K^+ (γ_{oc}) (mg/plant)				Transport index $= (\frac{\gamma_{cx}}{\gamma_{oc}} \times 100)$			
	Control	ABA			Control	ABA			Control	ABA		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.481 ±0.049	0.474 ±0.041	0.438 ±0.053	0.447 ±0.061	0.514 ±0.053	0.513 ±0.040	0.464 ±0.058	0.480 ±0.069	93.57	92.39	94.39	93.12
0-6	0.585 ±0.020	0.553 ±0.050	0.559 ±0.073	0.425 ±0.034	0.628 ±0.018	0.584 ±0.058	0.591 ±0.067	0.465 ±0.029	93.15	94.69	94.58	91.39
0-24	0.630 ±0.026	0.503 ±0.006	0.546 ±0.020	0.576 ±0.023	0.669 ±0.020	0.537 ±0.006	0.580 ±0.024	0.609 ±0.019	94.17	93.66	94.13	94.58
0-48	0.591 ±0.059	0.588 ±0.061	0.556 ±0.027	0.518 ±0.018	0.641 ±0.061	0.637 ±0.061	0.598 ±0.031	0.552 ±0.017	92.19	92.30	92.97	93.84

transport index of K^+ at 6 hours of treatment but increased that at 48 hours of treatment and did not show any significant effect at 3 and 24 hours of treatment (Table 2).

In intact rice seedlings, 10^{-7} M ABA did not show any significant effect on net influx (γ_{OC}) of Na^+ (Table 3). 10^{-6} M ABA inhibited net influx of Na^+ by 14.7% at 3 hours of treatment (Table 3). 10^{-5} M ABA also inhibited net influx of Na^+ by 12.7, 10.9 and 12.4% at 3, 6 and 48 hours of treatment respectively (Table 3).

ABA (10^{-7} M) decreased long distance transport (γ_{CX}) of Na^+ in intact rice seedlings by 12.5 and 9.2% at 3 and 24 hours of treatment respectively (Table 3). 10^{-6} M ABA decreased long distance transport of Na^+ by 11.1 to 9.2% at 24 to 48 hours of treatment (Table 3). At the concentration of 10^{-5} M, ABA decreased long distance transport of Na^+ by 12.5% at 6 hours of treatment in intact seedlings (Table 3).

ABA (10^{-7} M) decreased transport index of Na^+ at 3, 24 and 48 hours of treatment except at 6 hours of treatment (Table 3). 10^{-6} M ABA decreased transport index of Na^+ at 6 to 48 hours treatment after an initial increase at 3 hours of treatment (Table 3). ABA (10^{-5} M) increased transport index of Na^+ in intact rice seedlings at 3, 24 and 48 hours of treatment except at 6 hours of treatment (Table 3).

Table 3. The effect of ABA on net influx and long distance transport of Na^+ in intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Table 2.

Time (hr)	Transport of Na^+ from root to shoot (γ_{cx}) (mg/shoot)				Net influx of Na^+ (γ_{oc}) (mg/plant)				Transport index $\frac{\gamma_{cx}}{\gamma_{oc}} \times 100$			
	Control	ABA			Control	ABA			Control	ABA		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.048 ±0.004	0.042 ±0.006	0.045 ±0.002	0.047 ±0.003	0.102 ±0.003	0.095 ±0.006	0.087 ±0.005	0.089 ±0.003	47.05	44.21	54.02	58.80
0-6	0.048 ±0.000	0.045 ±0.000	0.045 ±0.000	0.042 ±0.000	0.101 ±0.002	0.094 ±0.000	0.096 ±0.003	0.090 ±0.003	47.52	47.87	46.87	46.66
0-24	0.054 ±0.000	0.049 ±0.005	0.048 ±0.005	0.052 ±0.003	0.100 ±0.004	0.092 ±0.006	0.095 ±0.006	0.094 ±0.002	54.00	53.26	50.52	55.31
0-48	0.054 ±0.001	0.055 ±0.002	0.049 ±0.002	0.050 ±0.000	0.105 ±0.003	0.111 ±0.003	0.100 ±0.006	0.092 ±0.002	51.42	49.54	49.00	54.34

4.3.4. The effect of ABA on net influx and long distance transport of divalent cations in intact rice seedlings

The intact rice seedlings, 10^{-7} M ABA decreased net influx (Ψ_{oc}) of Ca^{2+} by 9.2 and 14.9% at 3 and 24 hours of treatment (Table 4). On the other hand, 10^{-6} M ABA increased net influx of Ca^{2+} by 9.2, 11.7 and 19.6% at 3, 6 and 48 hours of treatment respectively (Table 4). 10^{-5} M ABA increased net influx of Ca^{2+} by 27.4 to 11.9% at 6 to 24 hours of treatment after an initial decrease at 3 hours of treatment (Table 4).

ABA (10^{-7} M) decreased long distance transport (Ψ_{cx}) of Ca^{2+} by 18.7% in intact seedlings at 24 hours of treatment (Table 4). 10^{-6} M ABA increased long distance transport of Ca^{2+} by 22.6, 11.4 and 35.7% at 3, 6 and 48 hours of treatment respectively except a decrease by 10.4% at 24 hours of treatment (Table 4). At the concentration of 10^{-5} M, ABA increased long distance transport of Ca^{2+} by 17.1% at 6 hours of treatment in intact seedlings (Table 4).

Transport index of Ca^{2+} increased by ABA (10^{-7}, 10^{-6} and 10^{-5} M) at 3 and 48 hours of treatment while decreased at 6 to 24 hours of treatment in intact rice seedlings (Table 4).

In intact rice seedlings, 10^{-7} M ABA increased net influx (Ψ_{oc}) of Mg^{2+} by 24.4 and 12.0% at 6 and 48 hours of treatment while it decreased by 11.7% at 3 hours of treatment (Table 5). 10^{-6} M ABA decreased net influx of Mg^{2+} by 13.7% at 3 hours of treatment (Table 5). 10^{-5} M ABA also decreased net influx of Mg^{2+} by 19.6%

Table 4. The effect of ABA on net influx and long distance transport of Ca^{2+} in intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Table 2.

Time (hr)	Transport of Na^{2+} from root to shoot (γ_{cx}) (mg/shoot)				Net influx of Na^{2+} (γ_{oc}) (mg/plant)				Transport index $= (\frac{\gamma_{cx}}{\gamma_{oc}} \times 100)$			
	Control	ABA			Control	ABA			Control	ABA		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.031 ±0.000	0.034 ±0.002	0.038 ±0.003	0.032 ±0.003	0.054 ±0.004	0.049 ±0.005	0.059 ±0.003	0.047 ±0.005	57.40	69.38	64.40	68.08
0-6	0.035 ±0.001	0.033 ±0.002	0.039 ±0.007	0.041 ±0.003	0.051 ±0.003	0.052 ±0.006	0.057 ±0.007	0.065 ±0.004	68.62	63.46	68.42	63.07
0-24	0.048 ±0.006	0.039 ±0.002	0.043 ±0.003	0.050 ±0.002	0.067 ±0.005	0.057 ±0.004	0.063 ±0.005	0.075 ±0.007	71.64	68.42	68.25	66.66
0-48	0.042 ±0.006	0.046 ±0.002	0.057 ±0.011	0.041 ±0.003	0.066 ±0.004	0.070 ±0.002	0.079 ±0.014	0.063 ±0.001	63.63	65.71	72.15	65.07

Table 5. The effect of ABA on net influx and long distance transport of Mg^{2+} in intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Table 2.

Time (hr)	Transport of Mg^{2+} from root to shoot (γ_{cx}) (mg/shoot)				Net influx of Mg^{2+} (γ_{oc}) (mg/plant)				Transport index $= (\frac{\gamma_{cx}}{\gamma_{oc}} \times 100)$			
	Control	ABA			Control	ABA			Control	ABA		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.037 ±0.002	0.033 ±0.001	0.033 ±0.002	0.031 ±0.003	0.051 ±0.001	0.045 ±0.002	0.044 ±0.003	0.041 ±0.004	72.54	73.33	75.00	75.60
0-6	0.033 ±0.000	0.040 ±0.002	0.036 ±0.002	0.031 ±0.003	0.045 ±0.002	0.056 ±0.002	0.049 ±0.004	0.042 ±0.003	73.33	71.42	73.46	73.80
0-24	0.045 ±0.002	0.038 ±0.001	0.046 ±0.011	0.037 ±0.002	0.057 +0.002	0.054 ±0.004	0.060 ±0.012	0.053 ±0.006	78.94	70.37	76.66	69.81
0-48	0.041 ±0.000	0.044 ±0.001	0.038 ±0.005	0.036 ±0.003	0.058 ±0.002	0.065 ±0.001	0.057 ±0.009	0.053 ±0.004	70.68	67.69	66.66	67.92

at 3 hours of treatment and the inhibitory effect was maintained up to 48 hours of treatment (Table 5).

ABA (10^{-7} M) decreased long distance transport (Ψ_{cx}) of Mg^{2+} by 10.8 and 15.5% at 3 and 24 hours of treatment while increased it by 21.2% at 6 hours of treatment (Table 5). At the concentration of 10^{-5} M, ABA decreased long distance transport of Mg^{2+} by 10.8% at 3 hours of treatment (Table 5). 10^{-5} M ABA also decreased long distance transport of Mg^{2+} by 16.2, 17.7 and 12.2% at 3, 6 and 48 hours of treatment respectively in intact seedlings (Table 5).

In intact seedlings, 10^{-7} M ABA decreased transport index of Mg^{2+} at 6 to 48 hours of treatment after an initial increase at 3 hours of treatment (Table 5). 10^{-6} M ABA increased transport index of Mg^{2+} at 3 to 6 hours of treatment but decreased at 24 to 48 hours of treatment (Table 5). Similarly, 10^{-5} M ABA increased transport index of Mg^{2+} at 3 to 6 hours of treatment but decreased it at 24 to 48 hours of treatment (Table 5).

In intact seedlings, 10^{-7} M ABA decreased net influx (Ψ_{oc}) of Fe^{2+} by 24.2 to 38.2% at 6 to 24 hours of treatment after an initial increase by 7.4% at 3 hours of treatment. The inhibitory effect was maintained up to 48 hours of treatment (Table 6). Similarly, 10^{-6} M ABA decreased net influx of Fe^{2+} by 24.2 to 11.7% at 6 to 24 hours of treatment and the inhibitory effect was maintained up to 48 hours of treatment (Table 6). 10^{-5} M ABA also decreased net influx of Fe^{2+} by 36.3, 17.6 and 21.6% at 6, 24 and 48 hours of treatment respectively (Table 6).

Table 6. The effect of ABA on net influx and long distance transport of Fe^{2+} in intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Table 2.

Time (hr)	Transport of Fe^{2+} from root to shoot (γ_{cx}) (mg/shoot)				Net influx of Fe^{2+} (γ_{oc}) (mg/plant)				Transport index $= (\frac{\gamma_{cx}}{\gamma_{oc}} \times 100)$			
	Control	ABA			Control	ABA			Control	ABA		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.010 ±0.000	0.012 ±0.002	0.013 ±0.000	0.011 ±0.000	0.029 ±0.003	0.029 ±0.003	0.025 ±0.003	0.027 ±0.004	37.03	41.37	52.00	40.74
0-6	0.010 ±0.000	0.012 ±0.000	0.012 ±0.000	0.011 ±0.000	0.033 ±0.005	0.025 ±0.001	0.025 ±0.001	0.021 ±0.006	30.30	48.00	48.00	52.38
0-24	0.015 ±0.000	0.011 ±0.000	0.012 ±0.000	0.015 ±0.001	0.034 ±0.004	0.021 ±0.003	0.030 ±0.002	0.028 ±0.002	44.11	52.38	40.00	53.57
0-48	0.015 ±0.003	0.014 ±0.001	0.015 ±0.001	0.013 ±0.001	0.037 ±0.005	0.034 ±0.003	0.035 ±0.001	0.029 ±0.001	40.54	41.17	42.85	44.82

ABA (10^{-7} M) increased long distance transport (Ψ_{CX}) of Fe^{2+} in intact seedlings by 20.0% from 3 to 6 hours of treatment but increased by 26.6% at 24 hours of treatment and the inhibitory effect was maintained up to 48 hours of treatment (Table 6). 10^{-6} M ABA increased long distance transport of Fe^{2+} by 30.0 to 20.0% at 3 to 6 hours of treatment but decreased at 24 hours of treatment (Table 6). 10^{-5} M ABA also increased long distance transport of Fe^{2+} by 10.0% at 3 to 6 hours of treatment but decreased by 13.3% at 48 hours of treatment (Table 6).

In intact rice seedlings, 10^{-7} M ABA increased transport index of Fe^{2+} at 3 to 48 hours of treatment (Table 6). 10^{-5} M ABA increased transport index of Fe^{2+} at 3, 6 and 48 hours of treatment but decreased it at 24 hours of treatment (Table 6). At the concentration of 10^{-5} M, ABA increased transport index of Fe^{2+} at 3 to 48 hours of treatment in intact seedlings (Table 6).

4.3.5. The effect of kinetin on the accumulation of monovalent cations in intact rice seedlings

In the root of intact rice seedlings, 10^{-7} M kinetin caused a gradual decrease of K^+ accumulation by 16.7 and 19.1% at 24 and 48 hours of treatment respectively after an initial promotion at 3 hours of treatment (Fig. 26a). 10^{-6} M kinetin increased K^+ accumulation by 26.3% at 3 hours of treatment followed by a decrease up to 24 hours of treatment and the accumulation of K^+ levelled up with the control at 48 hours of treatment (Fig. 26a). At the concentration of 10^{-5} M, kinetin inhibited K^+ accumulation

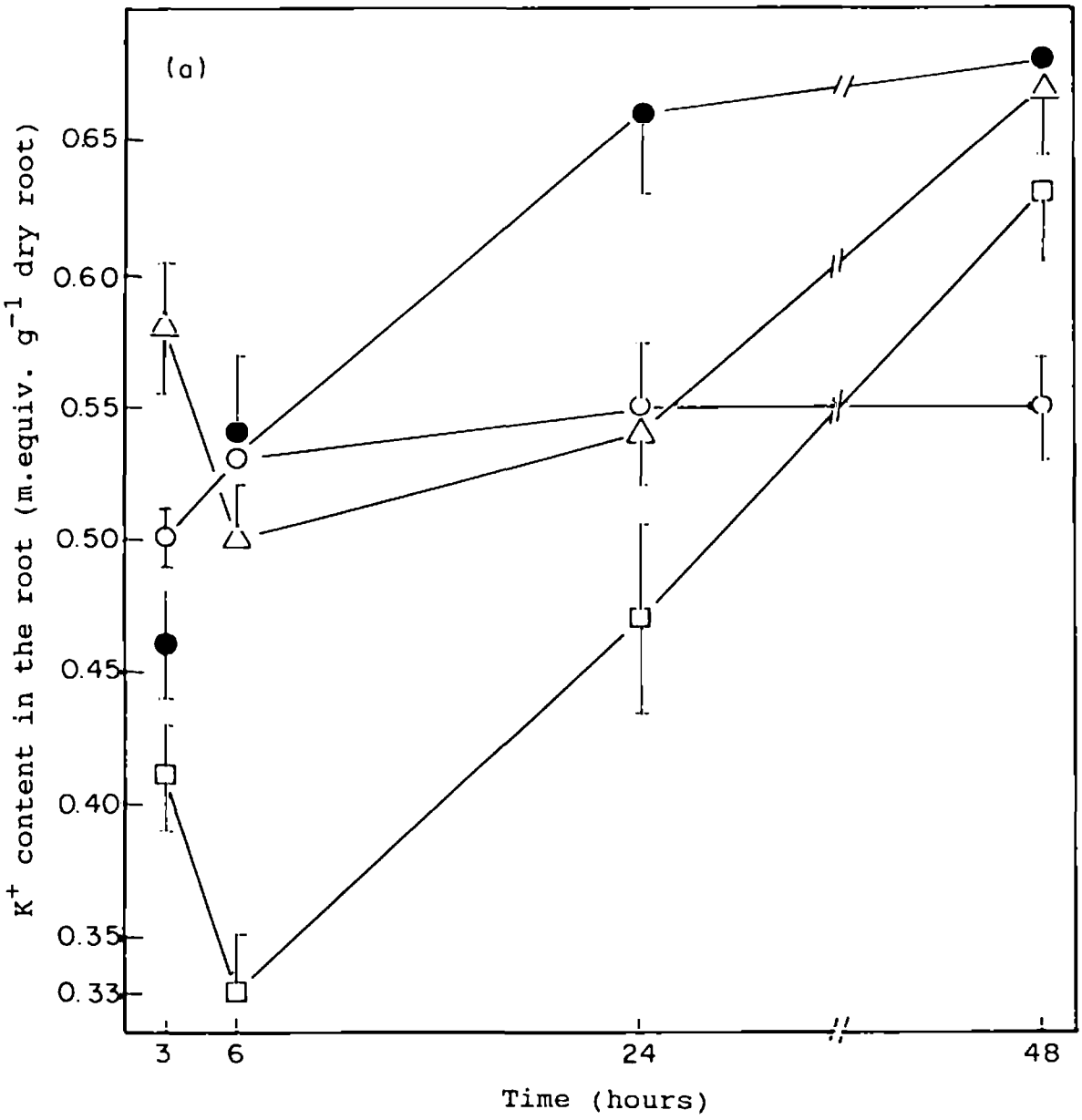

Fig. 26a. The effect of different concentrations of kinetin on K^+ accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

in the root of intact seedlings by 10.5, 39.7 and 29.1% at 3, 6 and 24 hours of treatment respectively (Fig. 26a).

In the shoot of intact rice seedlings, kinetin (10^{-7} and 10^{-6} M) did not show any significant effect on K^+ accumulation (Fig. 26b). On the other hand, 10^{-5} M kinetin increased K^+ accumulation by 20.4, 10.1, 8.0 and 15.7% at 3, 6, 24 and 48 hours of treatment respectively in the root of intact seedlings (Fig. 26b).

In the root of intact rice seedlings, 10^{-7} M kinetin gradually decreased Na^+ accumulation by 12.4 to 25.4% at 3 to 24 hours of treatment while it increased Na^+ accumulation by 23.0% at 48 hours of treatment (Fig. 27a). 10^{-6} M kinetin increased Na^+ accumulation by 9.4 and 20.3% at 3 and 48 hours of treatment respectively (Fig. 27a). At the concentration of 10^{-5} M kinetin caused an increase in Na^+ accumulation in the root of intact seedlings by 20.3% at 3 hours of treatment and the stimulatory effect was maintained up to 48 hours of treatment (Fig. 27a).

In the shoot of intact rice seedlings, 10^{-7} M kinetin decreased Na^+ accumulation by 25.0 to 8.3% at 3 to 24 hours of treatment and was levelled with the control at 48 hours of treatment (Fig. 27b). At the concentration of 10^{-6} M, kinetin also inhibited Na^+ accumulation by 39.6 to 13.3% at 3 to 24 hours of treatment except an increase at 48 hours of treatment (Fig. 27b). Similarly, 10^{-5} M kinetin decreased Na^+ accumulation by 12.2, 27.1 and 18.8% at 3, 6 and 24 hours of treatment respectively in

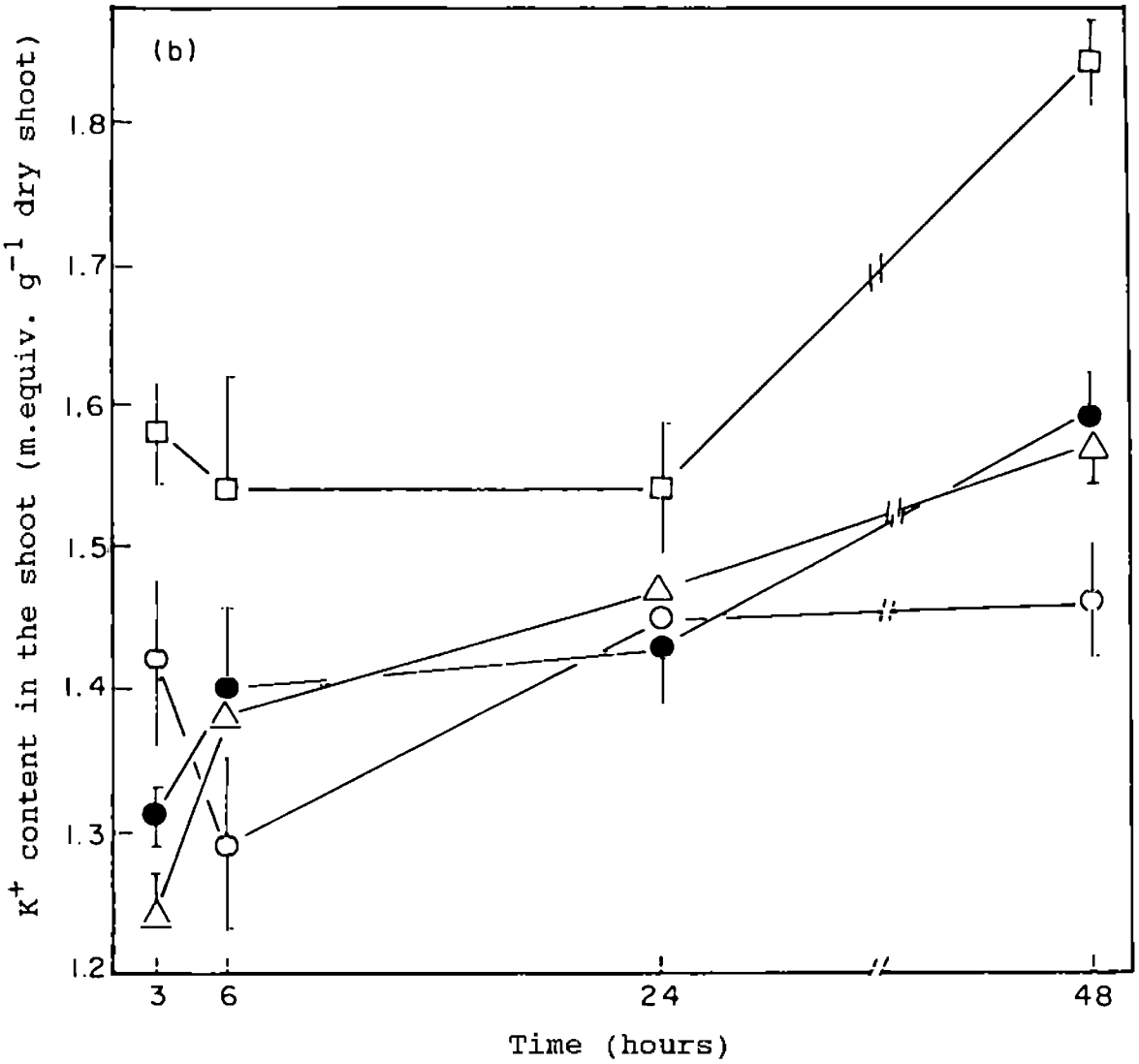

Fig. 26b. The effect of different concentrations of kinetin on K^+ accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

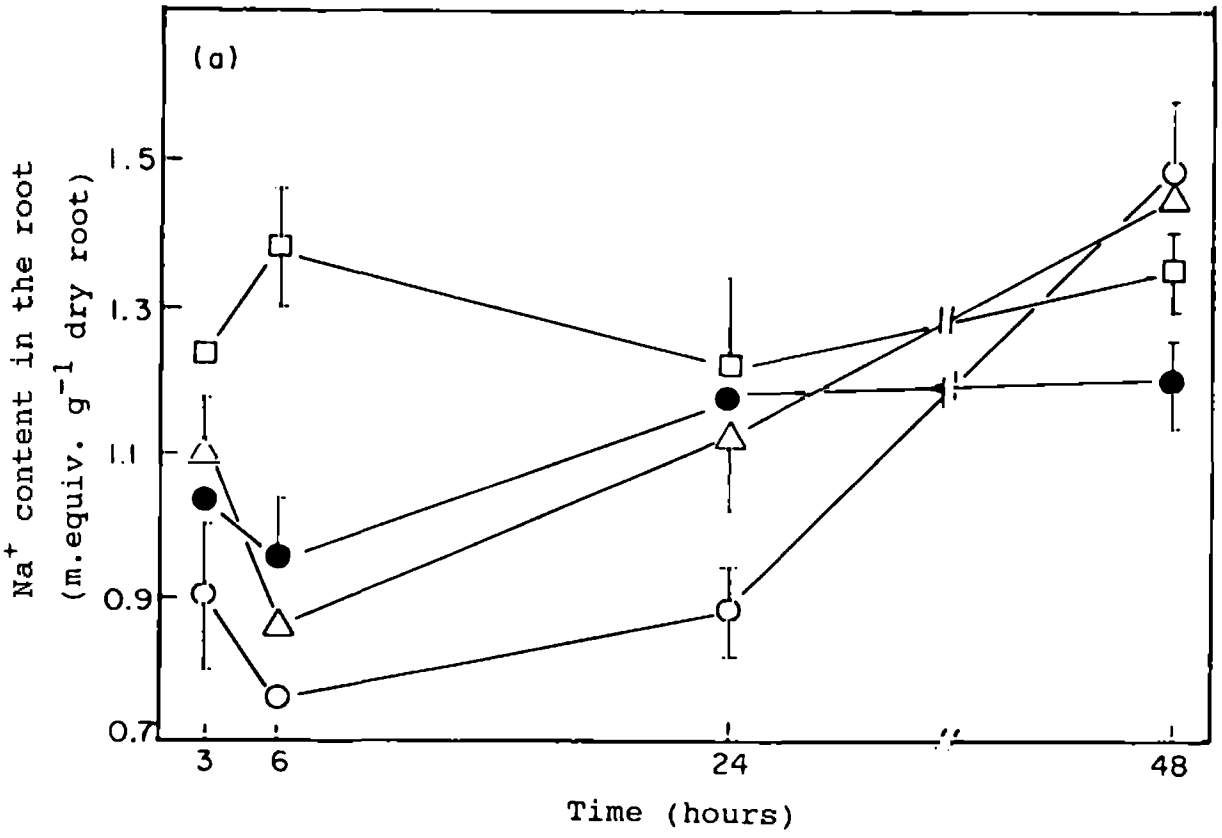

Fig. 27a. The effect of different concentrations of kinetin on Na^+ accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

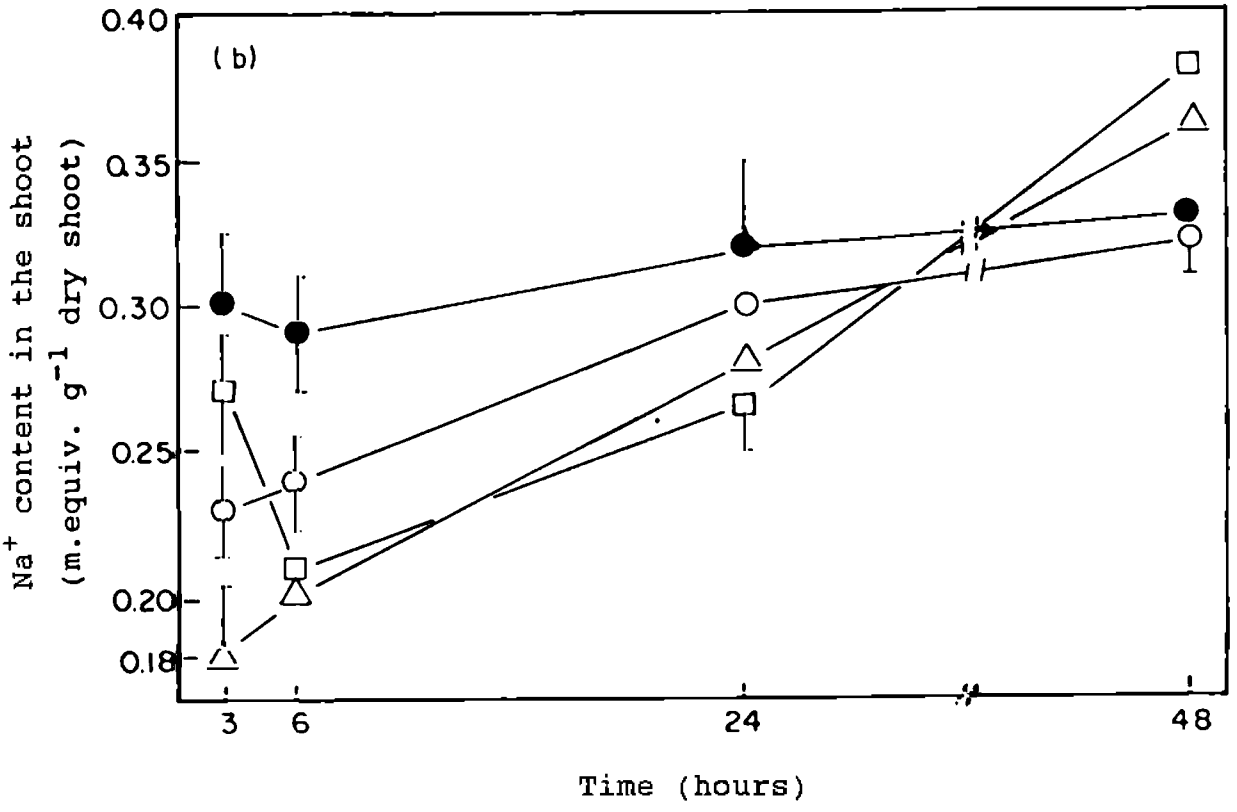

Fig. 27b. The effect of different concentrations of kinetin on Na^+ accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

the shoot of intact seedlings except an increase at 48 hours of treatment (Fig. 27b).

4.3.6. The effect of kinetin on the accumulation of divalent cations in intact rice seedlings

In the root of intact rice seedlings, 10^{-7} M kinetin inhibited Ca^{2+} accumulation by 25.7% at 3 hours of treatment whereas it stimulated Ca^{2+} accumulation by 21.2 and 13.1% at 6 and 48 hours of treatment respectively (Fig. 28a). Kinetin, at 10^{-6} M, also caused an inhibition in Ca^{2+} accumulation by 34.4% at 3 hours of treatment and the inhibitory effect gradually declined leading to a stimulation of Ca^{2+} accumulation by 34.2% at 48 hours of treatment (Fig. 28a). At the concentration of 10^{-5} M, kinetin caused an increase in Ca^{2+} accumulation by 17.9 to 8.1% at 6 to 48 hours of treatment after an initial inhibition of 20.7% at 3 hours of treatment in the root of intact seedlings (Fig. 28a).

In the shoot of intact rice seedlings, 10^{-7} M kinetin decreased Ca^{2+} accumulation by 16.1, 31.9 and 22.7% at 3, 24 and 48 hours of treatment (Fig. 28b). 10^{-6} M kinetin also decreased Ca^{2+} accumulation by 27.2, 8.3, 20.2 and 15.4% at 3, 6, 24 and 48 hours of treatment respectively (Fig. 28b). At the concentration of 10^{-5} M, kinetin caused a decrease in Ca^{2+} accumulation by 12.9 to 12.6% at 6 to 48 hours of treatment after an initial increase at 3 hours of treatment in the shoot of intact seedlings (Fig. 28b).

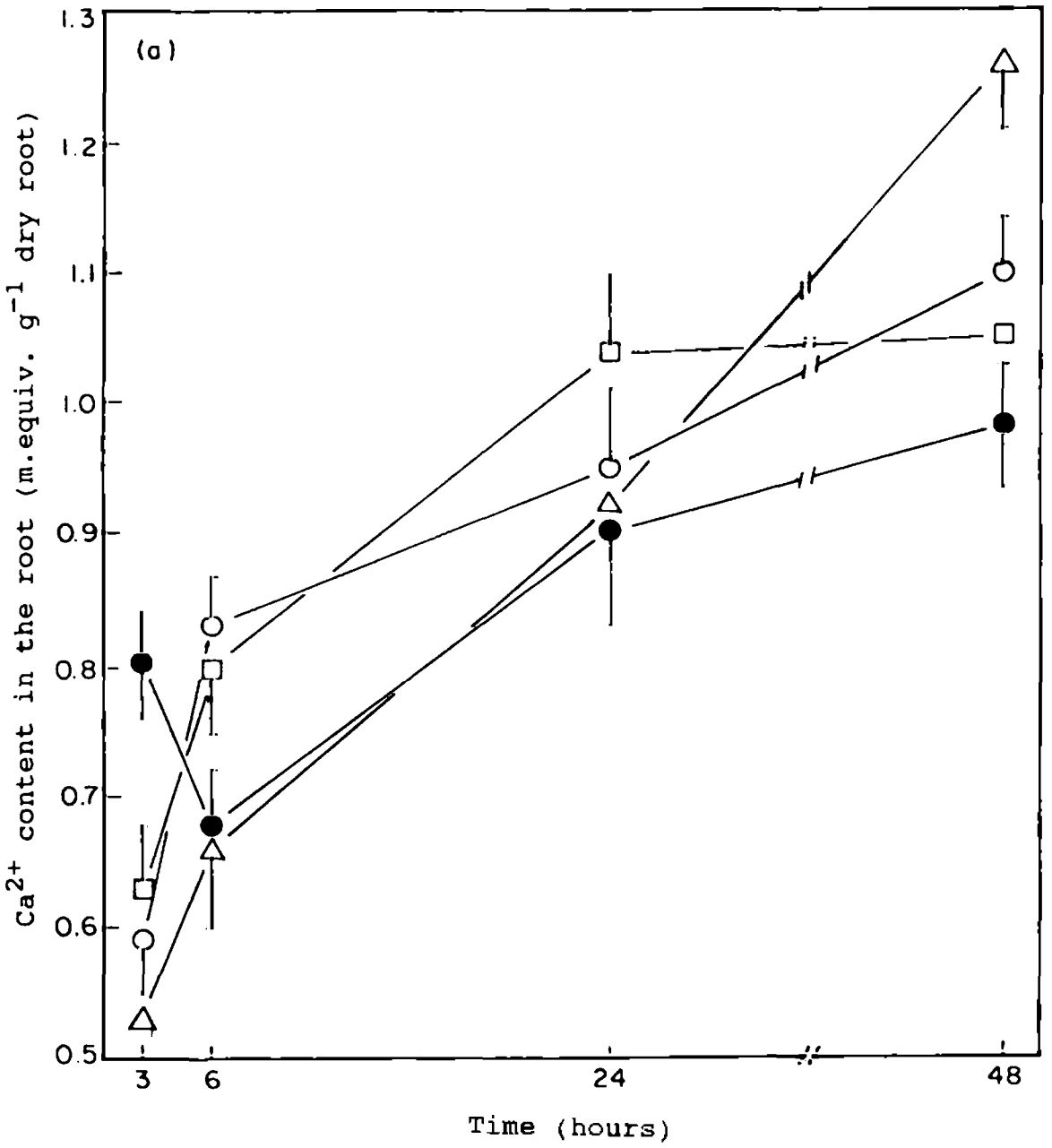

Fig. 28a. The effect of different concentrations of kinetin on Ca^{2+} accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

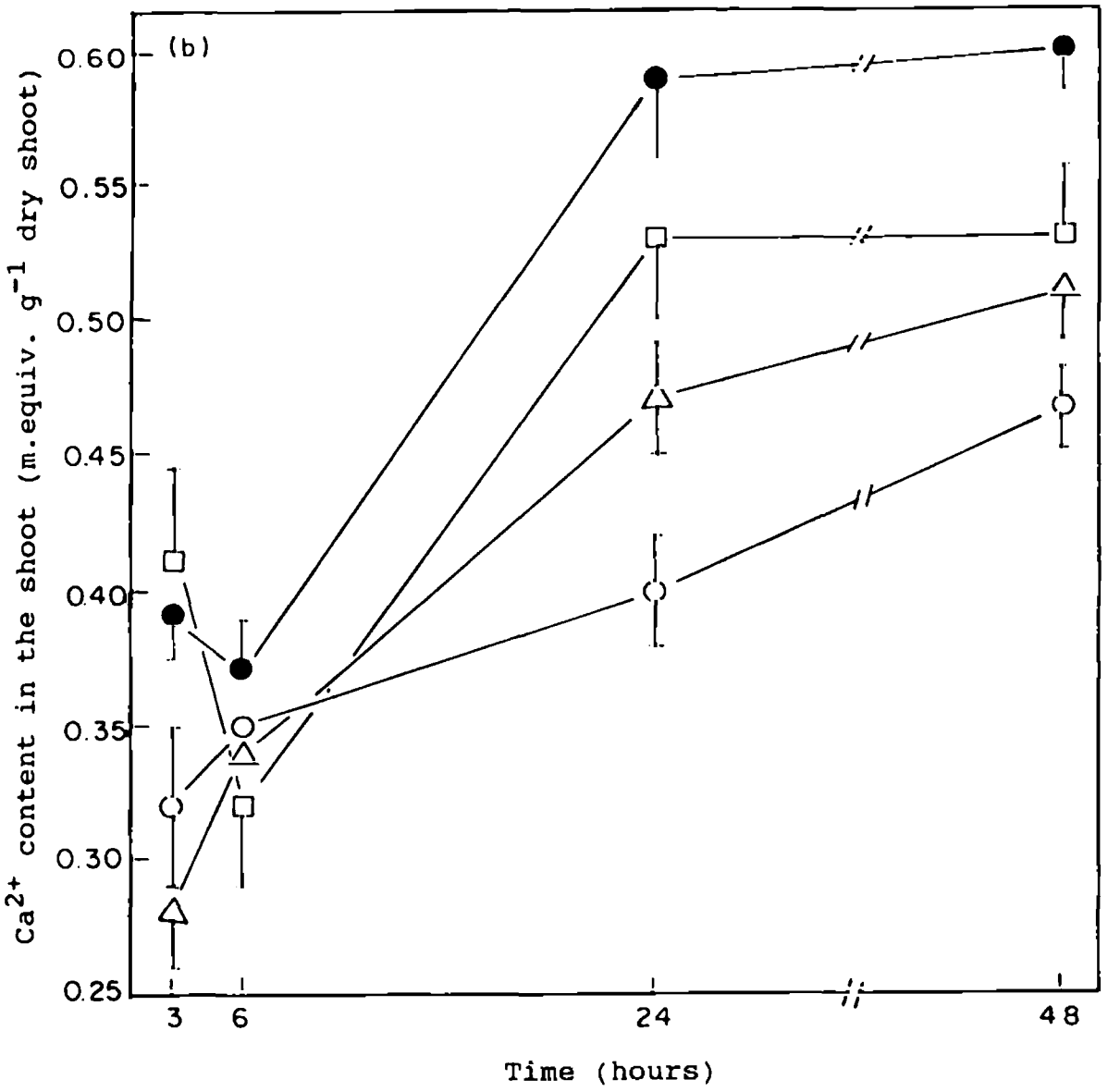

Fig. 28b. The effect of different concentrations of kinetin on Ca^{2+} accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

In the root of intact rice seedlings, 10^{-7} M kinetin caused an inhibition of Mg^{2+} accumulation by 15.8% at 3 hours of treatment while it caused an increase by 82.0% at 6 hours of treatment. This stimulatory effect was maintained up to 48 hours of treatment (Fig. 29a). 10^{-6} M kinetin decreased Mg^{2+} accumulation by 36.6 to 27.6% at 3 to 6 hours of treatment followed by an increase of 21.3% at 24 hours of treatment and the rate of Mg^{2+} accumulation was levelled with the control at 48 hours of treatment (Fig. 29a). At the concentration of 10^{-5} M, kinetin caused a decrease in Mg^{2+} accumulation by 42.6% at 3 hours of treatment followed by an increase of 73.3 to 10.0% at 6 to 24 hours of treatment and the rate of Mg^{2+} accumulation was levelled with the control at 48 hours of treatment in the root of intact seedlings (Fig. 29a).

In the shoot of intact rice seedlings, 10^{-7} M kinetin inhibited Mg^{2+} accumulation by 10.2% at 3 hours of treatment but stimulated Mg^{2+} accumulation by 11.6% at 6 hours of treatment and Mg^{2+} accumulation was levelled with the control at 48 hours of treatment (Fig. 29b). On the other hand, 10^{-6} and 10^{-5} M kinetin did not show any significant effect on Mg^{2+} accumulation in the shoot of intact seedling except at 3 hours of treatment. 10^{-6} M kinetin increased Mg^{2+} accumulation by 12.6% while 10^{-5} M kinetin decreased Mg^{2+} accumulation by 24.3% at 3 hours of treatment (Fig. 29b).

In the root of intact rice seedlings, 10^{-7} M kinetin did not show any significant effect up to 24 hours of treatment but it

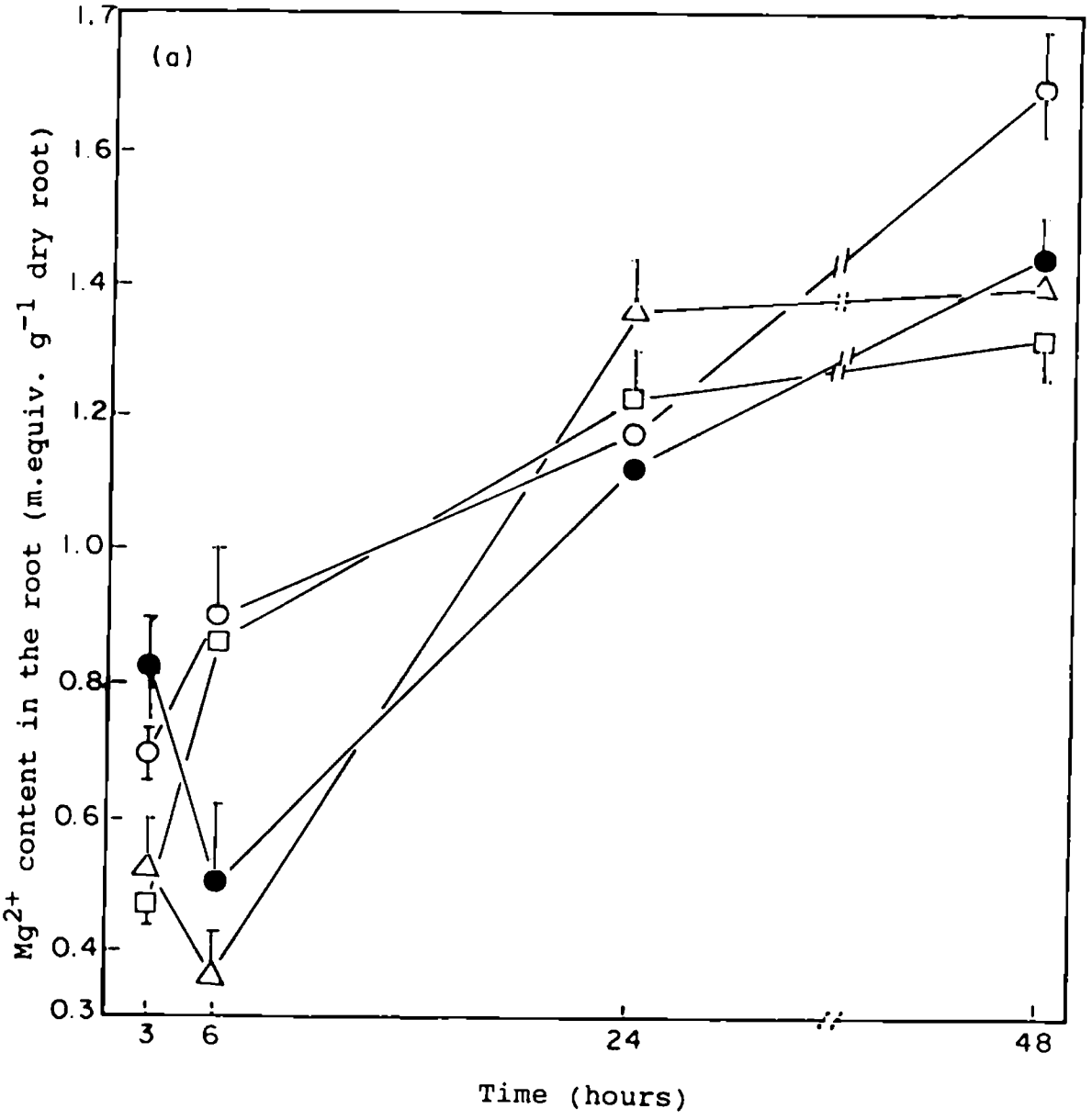

Fig. 29a. The effect of different concentrations of kinetin on Mg^{2+} accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

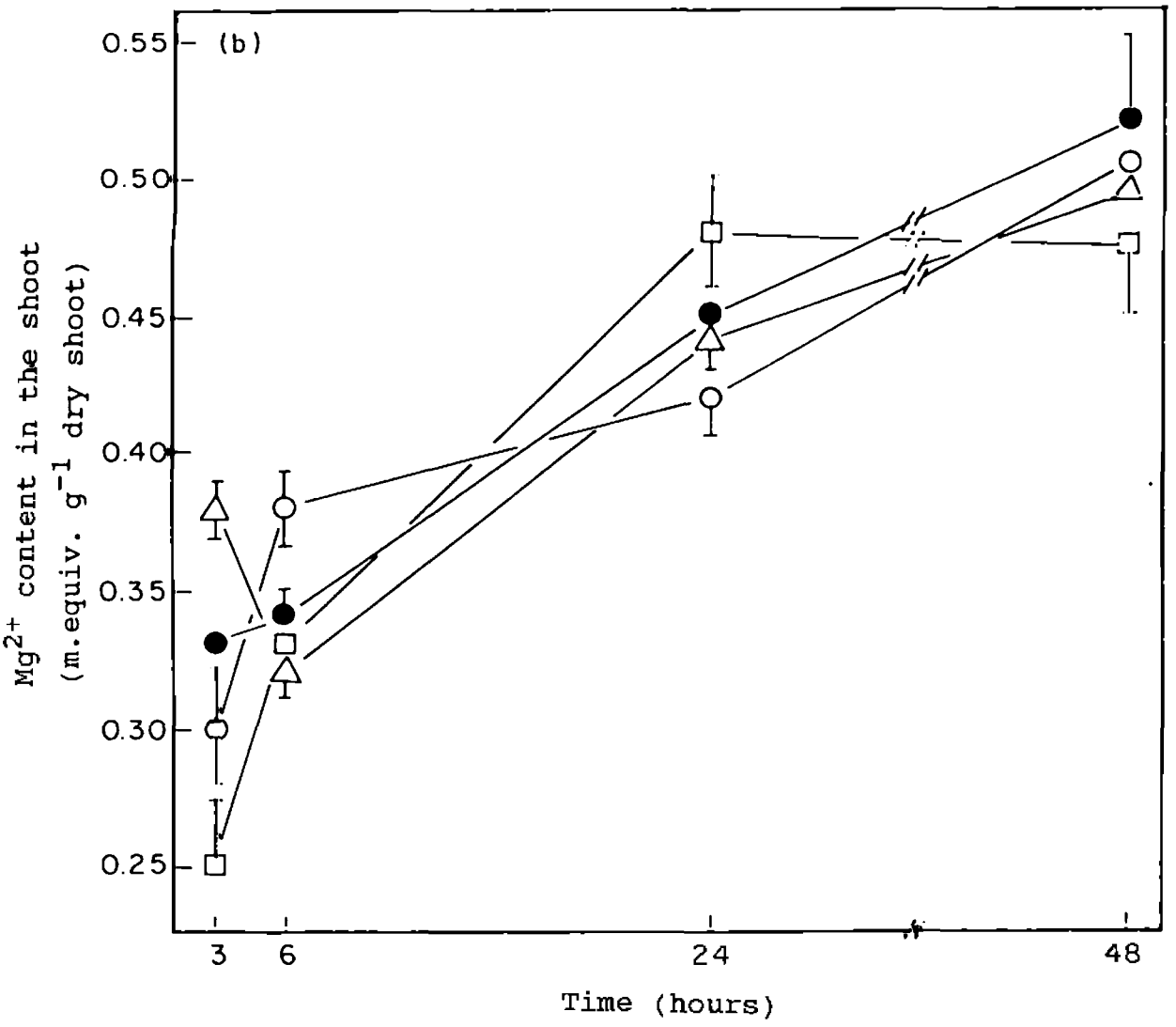

Fig. 29b. The effect of different concentrations of kinetin on Mg^{2+} accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

stimulated Fe^{2+} uptake by 32% at 48 hours of treatment (Fig. 30a). Kinetin, at 10^{-6} M, stimulated Fe^{2+} accumulation by 21.1, 12.6 and 10.7% at 3, 24 and 48 hours of treatment respectively (Fig. 30a). At the concentration of 10^{-5} M, kinetin showed stimulatory effect on Fe^{2+} accumulation at 3 to 24 hours of treatment and it was levelled with the control at 48 hours of treatment in the root of intact seedlings (Fig. 30a).

In the shoot of intact rice seedlings, kinetin (10^{-7}, 10^{-6} and 10^{-5} M) increased the accumulation of Fe^{2+} at 3 to 48 hours of treatment. The stimulation of Fe^{2+} accumulation ranged from 14.0 to 37.0% (Fig. 30b).

4.3.7. The effect of kinetin on net influx and long distance transport of monovalent cations in intact rice seedlings

In intact rice seedlings, kinetin (10^{-7} and 10^{-6} M) slightly depressed net influx (γ_{oc}) of K^+ (Table 7) but higher concentration of kinetin (10^{-5} M) decreased net influx of K^+ by 17.8% at 3 hours of treatment. This inhibitory effect was gradually nullified leading to a 12.9% increase at 48 hours of treatment (Table 7).

Kinetin (10^{-7} and 10^{-6} M) did not show any significant effect on long distance transport (γ_{cx}) of K^+ in intact seedlings (Table 7). On the other hand, higher concentration of kinetin (10^{-5} M) decreased long distance transport of K^+ by 16.0% at 3 hours of treatment. This inhibitory effect was gradually

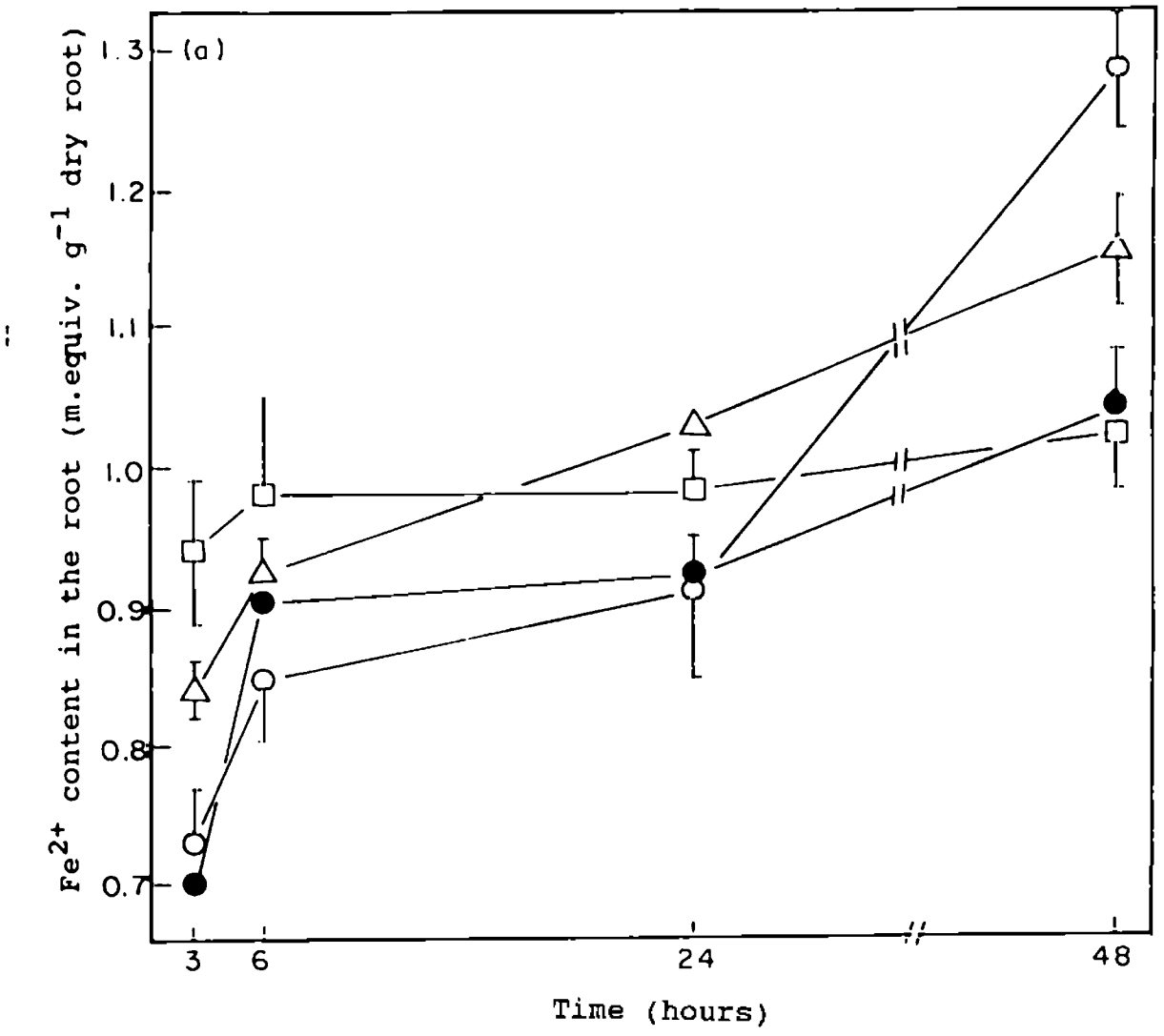

Fig. 30a. The effect of different concentrations of kinetin on Fe^{2+} accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

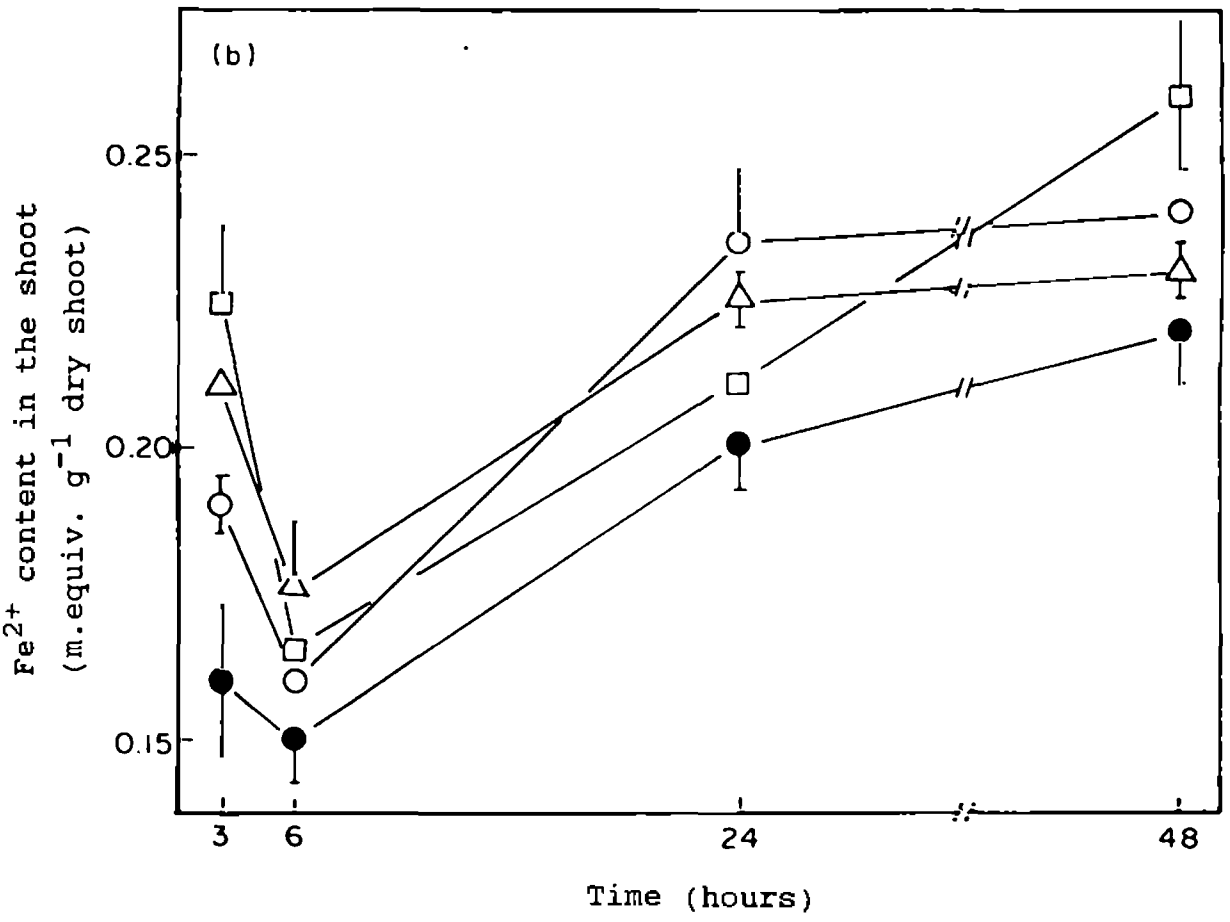

Fig. 30b. The effect of different concentrations of kinetin on Fe^{2+} accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

Table 7. The effect of kinetin on net influx and long distance transport of K^+ in intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Each value is the mean of three replicates; ± represents standard error.

Time (hr)	Transport of K^+ from root to shoot (γ_{cx}) (mg/shoot)				Net influx of K^+ (γ_{oc}) (mg/plant)				Transport index $= (\frac{\gamma_{cx}}{\gamma_{oc}} \times 100)$			
	Control	Kinetin			Control	Kinetin			Control	Kinetin		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.406 ±0.014	0.385 ±0.025	0.370 ±0.034	0.341 ±0.040	0.432 ±0.014	0.410 ±0.024	0.396 ±0.033	0.355 ±0.040	93.98	93.90	93.43	96.05
0-6	0.426 ±0.013	0.425 ±0.012	0.405 ±0.010	0.445 ±0.005	0.462 ±0.011	0.455 ±0.007	0.435 ±0.013	0.460 ±0.005	92.20	93.40	93.10	96.73
0-24	0.435 ±0.025	0.428 ±0.060	0.436 ±0.023	0.431 ±0.006	0.458 ±0.017	0.464 ±0.061	0.475 ±0.027	0.452 ±0.006	94.97	92.24	91.78	95.35
0-48	0.476 ±0.039	0.478 ±0.061	0.520 ±0.026	0.543 ±0.034	0.516 ±0.038	0.512 ±0.061	0.551 ±0.022	0.583 ±0.035	92.24	93.35	94.37	93.13

nullified leading to a 14.0% increase at 48 hours of treatment (Table 7).

Kinetin (10^{-7} and 10^{-6} M) did not show any significant effect on transport index of K^+ at 3 hours of treatment but decreased that at 24 hours of treatment while increased that at 6 and 48 hours of treatment (Table 7). On the other hand, 10^{-5} M kinetin increased transport index of K^+ at 3 to 48 hours of treatment in intact rice seedlings (Table 7).

In intact seedlings, 10^{-7} M kinetin inhibited net influx (Ψ_{oc}) of Na^+ by 30.0 to 17.3% at 3 to 24 hours of treatment. The inhibitory effect gradually declined and ultimately led to a stimulation of 17.7% at 48 hours of treatment (Table 8). Similarly, 10^{-6} M kinetin inhibited net influx of Na^+ by 30.0 to 30.6% at 3 to 6 hours of treatment but increased by 15.6% at 48 hours of treatment (Table 8). 10^{-5} M kinetin also inhibited net influx of Na^+ by 33.3, 19.3 and 22.4% at 3, 6 and 24 hours of treatment respectively whereas it increased that at 48 hours of treatment by 20.8% (Table 8).

Kinetin (10^{-7} M) inhibited long distance transport (Ψ_{cx}) of Na^+ in intact seedlings by 34.5, 9.8 and 10.5% at 3, 6 and 24 hours of treatment respectively (Table 8). 10^{-6} M kinetin decreased long distance transport of Na^+ by 43.6 to 15.7% at 3 to 24 hours of treatment. This inhibitory effect gradually declined and ultimately stimulated at 48 hours of treatment by 22.8% (Table 8). 10^{-5} M kinetin also decreased long distance transport

Table 8. The effect of kinetin on net influx and long distance transport of Na^+ in intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Table 7.

Time (hr)	Transport of Na^+ from root to shoot (γ_{cx}) (mg/shoot)				Net influx of Na^+ (γ_{oc}) (mg/plant)				Transport index $\frac{\gamma_{cx}}{\gamma_{oc}} \times 100$			
	Control	Kinetin			Control	Kinetin			Control	Kinetin		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.055 ±0.010	0.036 ±0.006	0.031 ±0.004	0.035 ±0.008	0.090 ±0.013	0.063 ±0.007	0.063 ±0.003	0.060 ±0.005	61.11	57.14	49.20	58.33
0-6	0.051 ±0.002	0.046 ±0.008	0.033 ±0.008	0.035 ±0.003	0.088 ±0.010	0.071 ±0.010	0.061 ±0.007	0.071 ±0.016	57.95	64.78	54.09	49.29
0-24	0.057 ±0.004	0.051 ±0.014	0.048 ±0.012	0.043 ±0.002	0.098 ±0.013	0.081 ±0.010	0.093 ±0.007	0.076 ±0.004	58.16	62.96	51.61	56.57
0-48	0.057 ±0.007	0.062 ±0.003	0.070 ±0.015	0.066 ±0.013	0.096 ±0.006	0.113 ±0.018	0.111 ±0.004	0.116 ±0.007	59.37	54.86	63.06	56.89

of Na^+ by 36.3 to 24.5% at 3 to 24 hours of treatment but increased that by 15.7% at 48 hours of treatment (Table 8).

Kinetin (10^{-7} M) inhibited transport index of Na^+ at 3 and 48 hours of treatment while it stimulated at 6 to 24 hours of treatment (Table 8). 10^{-6} M kinetin also inhibited transport index of Na^+ at 3 to 24 hours of treatment but stimulated at 48 hours of treatment (Table 8). 10^{-5} M kinetin inhibited transport index of Na^+ at 3 to 48 hours of treatment in intact rice seedlings (Table 8).

4.3.8. The effect of kinetin on net influx and long distance transport of divalent cations in intact rice seedlings

In intact rice seedlings, 10^{-7} M kinetin inhibited net influx (Ψ_{OC}) of Ca^{2+} by 26.5 and 21.5% at 3 and 24 hours of treatment respectively (Table 9). 10^{-6} M kinetin also inhibited net influx of Ca^{2+} by 33.7 to 11.2% at 3 to 24 hours of treatment and the inhibitory effect was maintained up to 48 hours of treatment (Table 9). Similarly, 10^{-5} M kinetin inhibited net influx of Ca^{2+} by 28.9 to 13.8% at 3 to 24 hours of treatment and the inhibitory effect was maintained up to 48 hours of treatment (Table 9).

Kinetin (10^{-7} M) decreased long distance transport (Ψ_{CX}) of Ca^{2+} by 26.6, 33.7 and 15.2% at 3, 24 and 48 hours of treatment respectively (Table 9). 10^{-6} M kinetin also inhibited long distance transport of Ca^{2+} by 30.0, 15.5 and 20.2% at 3, 6 and 24 hours of treatment respectively and was maintained up to 48 hours

Table 9. The effect of kinetin on net influx and long distance transport of Ca^{2+} in intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Each value is the mean of three replicates. ± represents standard error.

Time (hr)	Transport of Ca^{2+} from root to shoot (γ_{cx}) (mg/shoot)				Net influx of Ca^{2+} (γ_{oc}) (mg/plant)				Transport index $\frac{\gamma_{cx}}{\gamma_{oc}} \times 100$			
	Control	Kinetin			Control	Kinetin			Control	Kinetin		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.060 ±0.005	0.044 ±0.002	0.042 ±0.004	0.048 ±0.001	0.083 ±0.003	0.061 ±0.006	0.055 ±0.005	0.059 ±0 002	72.28	72.13	76.36	81.35
0-6	0.058 ±0.003	0.059 ±0.001	0.049 ±0.017	0.047 ±0.009	0.081 ±0.003	0.083 ±0.001	0.068 ±0.017	0.067 ±0.009	71.60	71.08	72.05	70.14
0-24	0.089 ±0.005	0.059 ±0.002	0.071 ±0.007	0.075 ±0.002	0.116 ±0.006	0.091 ±0.000	0.103 ±0.014	0.100 ±0.001	76.72	64.83	68.93	75.00
0-48	0.092 ±0.001	0.078 ±0.001	0.086 ±0.001	0.079 ±0.004	0.121 ±0.001	0.112 ±0.003	0.117 ±0.001	0.114 ±0.003	76.03	69.64	73.50	69.29

of treatment (Table 9). At the concentration of 10^{-5} M, kinetin decreased long distance transport of Ca^{2+} in intact rice seedlings by 20.0 to 14.1% at 3 to 48 hours of treatment (Table 9).

Kinetin, at the concentration of 10^{-7} M, decreased transport index of Ca^{2+} at 24 and 48 hours of treatment but did not show any significant effect at 3 and 6 hours of treatment (Table 9). 10^{-6} M kinetin also decreased transport index of Ca^{2+} at 24 and 48 hours except an increase at 3 and 6 hours of transport (Table 9). At 10^{-5} M, kinetin decreased transport index of Ca^{2+} at 6 to 48 hours of treatment after an initial increase at 3 hours of treatment in intact seedlings (Table 9).

Kinetin, at 10^{-7} M, increased net influx (Ψ_{OC}) of Mg^{2+} in intact rice seedlings by 28.5 and 12.3% at 6 and 48 hours of treatment respectively after an initial decrease by 22.2% at 3 hours of treatment (Table 10). On the other hand, 10^{-6} M kinetin decreased net influx of Mg^{2+} by 9.0 to 16.7% at 3 to 6 hours of treatment (Table 10). 10^{-5} M kinetin also decreased net influx of Mg^{2+} by 48.9% at 3 hours of treatment and the inhibitory effect was maintained up to 48 hours of treatment (Table 10).

Kinetin, at 10^{-7} M, decreased long distance transport (Ψ_{CX}) of Mg^{2+} by 22.6% at 3 hours of treatment but increased that by 18.7% at 6 hours of treatment (Table 10). 10^{-6} M kinetin did not show any significant effect on long distance transport of Mg^{2+} in intact rice seedlings (Table 10). At the concentration of 10^{-5} M, kinetin decreased long distance transport of Mg^{2+} by

Table 10. The effect of kinetin on net influx and long distance transport of Mg^{2+} in intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Table 7.

Time (hr)	Transport of Mg^{2+} from root to shoot (γ_{CA}) (mg/shoot)				Net influx of Mg^{2+} (γ_{oc}) (mg/plant)				Transport index $= (\frac{\gamma_{cx}}{\gamma_{oc}} \times 100)$			
	Control	Kinetin			Control	Kinetin			Control	Kinetin		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.031 ±0.009	0.024 ±0.004	0.034 ±0.002	0.019 ±0.008	0.045 ±0.006	0.035 ±0.003	0.041 ±0.002	0.023 ±0.008	68.88	68.57	82.92	82.60
0-6	0.032 ±0.002	0.038 ±0.001	0.029 ±0.002	0.029 ±0.005	0.042 ±0.002	0.054 ±0.001	0.035 ±0.002	0.041 ±0.002	76.19	70.37	82.85	70.73
0-24	0.041 ±0.002	0.038 ±0.005	0.040 ±0.001	0.041 ±0.004	0.061 ±0.002	0.062 ±0.002	0.069 ±0.012	0.059 ±0.005	67.21	61.29	57.97	69.49
0-48	0.048 ±0.002	0.050 ±0.000	0.050 ±0.001	0.043 ±0.005	0.073 ±0.002	0.082 ±0.003	0.071 ±0.001	0.068 ±0.004	65.75	60.97	70.42	63.23

38.7, 9.4 and 10.4% at 3, 6 and 48 hours of treatment respectively (Table 10).

In intact rice seedlings, transport index of Mg^{2+} was decreased by 10^{-7} M kinetin at 3 to 48 hours of treatment (Table 10). On the contrary, 10^{-6} M kinetin increased transport index of Mg^{2+} at 3, 6 and 48 hours of treatment (Table 10). Kinetin, at 10^{-5} M, decreased transport index of Mg^{2+} in intact seedling at 6 and 48 hours of treatment after an initial increase at 3 hours of treatment (Table 10).

Kinetin at the concentration of 10^{-7} M, increased net influx (Ψ_{OC}) of Fe^{2+} in intact rice seedlings by 12.1 to 21.8% at 24 to 48 hours of treatment (Table 11). 10^{-6} M kinetin also increased net influx of Fe^{2+} by 13.8 and 19.5% at 3 and 24 hours of treatment (Tale 11). On the other hand, 10^{-5} M kinetin caused a decrease in net influx of Fe^{2+} by 9.2 to 10.0% at 3 to 24 hours of treatment in intact seedlings (Table 11).

In intact rice seedlings, 10^{-7} M kinetin caused an increase in long distance transport (Ψ_{CX}) of Fe^{2+} by 25.0, 13,9 and 19.1% at 6, 24 and 48 hours of treatment respectively (Table 11). 10^{-6} M kinetin also increased long distance transport of Fe^{2+} by 25.0, 9.3 and 17.0% at 3, 24 and 48 hours of treatment respectively (Table 11). At 10^{-5} M, kinetin increased long distance transport by 17.0% at 48 hours of treatment (Table 11).

In intact rice seedlings, transport index of Fe^{2+} increased at 3 to 24 hours of treatment following 10^{-7} M kinetin treatment

Table 11. The effect of kinetin on net influx and long distance transport of Fe^{2+} in intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Table 7.

Time (hr)	Transport of Fe^{2+} from root to shoot (γ_{cx}) (mg/shoot)				Net influx of Fe^{2+} (γ_{oc}) (mg/plant)				Transport index $= (\frac{\gamma_{cx}}{\gamma_{oc}} \times 100)$			
	Control	Kinetin			Control	Kinetin			Control	Kinetin		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.036 ±0.002	0.036 ±0.000	0.045 ±0.002	0.036 ±0.003	0.065 ±0.002	0.062 ±0.003	0.074 ±0.002	0.059 ±0.001	55.38	58.06	60.81	61.01
0-6	0.032 ±0.000	0.040 ±0.003	0.037 ±0.001	0.034 ±0.003	0.074 ±0.001	0.075 ±0.003	0.075 ±0.006	0.066 ±0.002	43.24	53.33	49.33	51.51
0-24	0.043 ±0.001	0.049 ±0.006	0.047 ±0.001	0.042 ±0.002	0.082 ±0.007	0.092 ±0.009	0.098 ±0.008	0.074 ±0.006	52.43	53.26	47.95	56.75
0-48	0.047 ±0.001	0.056 ±0.006	0.055 ±0.002	0.055 ±0.000	0.096 ±0.004	0.117 ±0.006	0.093 ±0.002	0.103 ±0.002	48.95	47.86	59.13	53.39

(Table 11). 10^{-6} M kinetin also increased transport index of Fe^{2+} at 3 to 48 hours of treatment except at 24 hours of treatment (Table 11). Similarly, 10^{-5} M kinetin increased transport index of Fe^{2+} at 3 to 48 hours of treatment in intact seedlings (Table 11).

4.4. Discussion

ABA inhibited K^+ accumulation after an initial increase in the root and also inhibited in the shoot of intact rice seedlings (Fig. 21a and 21b). Similarly, ABA was found to decrease K^+ transport in the guttation fluid from passive hydathods of barley seedlings (Dieffenbach *et al.* 1980), in the root of intact maize seedlings (Shanner and co-workers 1975), in the shoot of intact *Hordeum vulgare* (Reidell and Schimid 1984) and in the root and shoot of intact bean seedlings (Karmoker and Van Steveninck 1979a).

ABA decreased Na^+ accumulation in the root and shoot of intact rice seedlings (Fig. 22a and 22b). Similarly, ABA induced inhibition of Na^+ accumulation in the root and shoot of intact bean seedlings (Karmoker and Van Steveninck 1979a).

ABA stimulated Ca^{2+} accumulation in the root and shoot of intact rice seedlings (Fig. 23a and 23b) ABA-induced stimulation of Ca^{2+} content was also reported in *Lemna gibba* when it was used at low concentration (Dekock *et al.* 1978).

ABA increased Mg^{2+} accumulation in the root of intact rice seedlings (Fig. 24a). The stimulatory effect of ABA on Mg^{2+} accumulation may be due to ABA-induced stimulation of energy metabolism which increased the activity of Mg^{2+} ATPase (Kasamo 1979). On the other hand, lower concentration of ABA (10^{-6} M) increased but higher concentration of ABA (10^{-5} M) decreased Mg^{2+} accumulation in the shoot of intact rice seedlings (Fig. 24b). It shows that higher concentration of ABA is inhibitory to Mg^{2+} accumulation in the shoot.

ABA decreased the accumulation of Fe^{2+} in the root of intact rice seedlings (Fig. 25a). On the other hand, ABA increased Fe^{2+} accumulation in the shoot of intact rice seedlings at 3 to 6 hours of treatment but inhibited that of Fe^{2+} accumulation at 24 hours of treatment (Fig. 25b). ABA-induced initial increase in Fe^{2+} accumulation is supported by Pandey and Kannan (1976). The inhibition in Fe^{2+} accumulation after 6 hours of treatment may be due to ABA-induced senescence of leaves (Addicott and Lyon 1969).

ABA decreased net influx (Ψ_{OC}) of K^+ in intact rice seedlings (Table 2). Similar effect of ABA on K^+ (^{86}Rb) influx was also reported in wheat root when ABA (40-80 μM) was added to the uptake solution. ABA also inhibited long distance transport of K^+ from root to shoot in intact rice seedlings (Table 2). Karmoker and Van Steveninck (1979a) reported that ABA inhibited long distance transport (Ψ_{CX}) of K^+ in intact bean seedlings. The uptake and long distance transport of ions in ABA-treated

seedlings may be controlled through a negative feedback system (Cram 1976).

ABA inhibited net influx (Ψ_{oc}) of Na^+ in intact rice seedlings (Table 3). ABA inhibited Na^+ transport from the root to the shoot in intact bean seedlings (Karmoker and Van Steveninck 1979a). Long distance transport (Ψ_{cx}) of Na^+ was also inhibited by ABA (Table 3). The inhibitory effect of ABA on long distance transport of Na^+ was supported by Karmoker and Van Steveninck (1978) who found that after an initial promotion, ABA inhibited long distance transport of ^{22}Na and total Na^+ in bean seedlings.

ABA (10^{-7} M) inhibited net influx (Ψ_{oc}) and long distance transport (Ψ_{cx}) of Ca^{2+} (Table 4). This indicates that ABA decrease the entry and mobilization of Ca^{2+}.

ABA (10^{-5} M) decreased both net influx (Ψ_{oc}) and long distance transport (Ψ_{cx}) of Mg^{2+} in intact rice seedlings (Table 5). This may be due to build up of supraoptimal concentration of endogenous ABA level due to continuous supply of ABA.

In intact rice seedlings, ABA inhibited net influx (Ψ_{oc}) but stimulated long distance transport (Ψ_{cx}) of Fe^{2+} (Table 6). This indicates that phytohormone increases transportation of Fe^{2+} to the shoot. This may help in increasing metabolic function in the shoot.

Kinetin decreased K^+ accumulation in intact roots of rice seedlings (Fig. 26a). On the other hand, kinetin (10^{-5} M) increased the accumulation of that ion in the shoot of intact

seedlings (Fig. 26b). Kinetin induced inhibition of K^+ accumulation was reported in the root of intact bean seedlings (Karmoker 1981), in the root of rice seedlings (Karmoker and Razia 1993) and in the root of intact radish seedlings (Bittner and Buschmann 1983).

Kinetin (10^{-5} M) stimulated Na^+ accumulation in the root of intact rice seedlings (Fig. 27a). On the other hand, kinetin decreased accumulation of that ion in the shoot of intact rice seedlings (Fig. 27b). This result indicates that kinetin increased tonoplast transport of Na^+ but inhibited the supply of Na^+ to the shoot. This is supported by Karmoker and Razia (1993) who found that kinetin increased Na^+ accumulation in the root of rice seedlings but decreased the transport of Na^+ to the shoot. Similar result was found in intact root of jute (Karmoker and Baten 1992).

Kinetin stimulated Ca^{2+} accumulation in the root of intact seedlings (Fig. 28a). On the other hand, kinetin caused an inhibition of Ca^{2+} accumulation in the shoot of intact rice seedlings (Fig. 28b). The stimulation of Ca^{2+} accumulation in the root and the inhibition of Ca^{2+} accumulation in the shoot may be due to increase in tonoplast transport and consequent decrease in the drainage of Ca^{2+} into the xylem.

Kinetin increased Mg^{2+} accumulation after an initial inhibition in the root of intact rice seedlings (Fig. 29a). The initial inhibition of Mg^{2+} accumulation by kinetin was also found in the

shoot of intact seedlings (Fig. 29b). The increase in Mg^{2+} accumulation may be due to kinetin-induced stimulation of Mg-ATPase activity (Przymusinski *et al.* 1981).

Kinetin increased Fe^{2+} accumulation both in the root and in the shoot of intact rice seedlings (Fig. 30a and 30b). Similarly, Pandey and Kannan (1976) showed that kinetin stimulated the transport of Fe^{2+} from root to the primary and trifoliate leaves when it was supplied to the roots.

Kinetin decreased both net influx (Ψ_{OC}) and long distance transport (Ψ_{CX}) of K^+ and Na^+ in intact rice seedlings (Table 7 and 8). This is supported by the work of Karmoker and Razia (1993) who also found a kinetin-induced inhibition of net influx and long distance transport of K^+ and Na^+. Similarly, kinetin was reported to inhibit the uptake and transport of ^{42}K in intact bean seedlings (Karmoker 1981) and barley roots (Dieffenbach *et al.* 1980).

Kinetin inhibited net influx (Ψ_{OC}) and long distance transport (Ψ_{CX}) of Ca^{2+} from root to the shoot of intact rice seedlings (Table 9). The decrease in Ca^{2+} will affect the permeability characteristics of plasmamembrane.

Kinetin (10^{-5} M) inhibited net influx (Ψ_{OC}) and long distance transport (Ψ_{CX}) of Mg^{2+}. On the other hand, 10^{-7} M kinetin increase that in rice seedlings (Table 10). Higher concentrations of kinetin may inhibited ion transport in some plants (Karmoker 1984). This indicates that lower concentration

of kinetin shows stimulatory effect but higher concentration shows inhibitory effect on net influx and long distance transport of Mg^{2+}.

In intact rice seedlings, 10^{-7} and 10^{-6} M kinetin stimulated net influx (Ψ_{oc}) and long distance transport (Ψ_{cx}) of Fe^{2+} from root to the shoot (Table 11). This indicates that kinetin may have regulate the pumping system of Fe^{2+} situated in the plasma membrane. The increase in long distance transport of Fe^{2+} may be due to increase in net influx of Fe^{2+} because increased accumulation of Fe^{2+} will lead to increased translocation of Fe^{2+} to the shoot.

CHAPTER 5

The effect of phytohormones on anions transport in intact rice seedings

5.1. Introduction

Phytohormones are very much active in regulating the anions transport in intact plants. Zholobak (1985) reported that GA or IAA swiftly promoted the influx of sulfate but their combined application decreased the influx of sulfate in 14-days-old pea plant. GA increased Cl^- content in mungbean leaves (Karmoker and Begum 1989).

Karmoker and Van Steveninck (1978) showed that ABA stimulated Cl^- accumulation in intact bean root. The net influx of Cl^- may be stimulated or remained unchanged by ABA. Dekock *et al.* (1978) reported that ABA stimulated nitrate content but inhibited phosphate content in *Lemna gibba*.

Torre and Liliana (1987) reported that kinetin decreased phosphate content in the cellular mass of *Chlorella pyrenoidosa* cultivars.

Karmoker (1981) observed a kinetin-induced inhibition of Cl^- in intact bean seedlings. Kinetin increased the net influx and long distance transport of Cl^- in intact jute seedlings (Karmoker and Baten 1992) whereas decreased in intact rice seedlings (Karmoker and Razia 1930).

There is a correlation between growth and ion transport in plant. Growth of a plant influences the demand for solutes which are essential to maintain the osmotic potential and to uphold metabolic activity as its volume increases (Sutcliffe 1976). Therefore, it is difficult to separate the effect of a phytohormone on growth from its effect on ion transport.

In this chapter, the effect of ABA and kinetin on anions transport in intact rice seedlings, the effect of ABA and kinetin on plant growth and the relationship between phytohormone-induced growth and ion transport in intact rice seedlings are reported.

5.2. Materials and Methods

5.2.1. Culture of plants

Plants were grown according to the method described in 2.4.

5.2.2. Methods of ion transport experiment with intact seedlings

Ion transport experiment was performed following the technique described in 2.6.

Stock solution of ABA or kinetin was prepared according to 2.3.4 or 2.3.5. ABA or kinetin was used at concentrations of 10^{-7}, 10^{-6} and 10^{-5} M.

5.2.3. Collection and drying of samples

Samples were collected and dried according to the method described in 2.7.

5.2.4. Methods of extraction of anions

Chloride and nitrate were extracted according to the method described in 2.8.2.

Phosphate was extracted following the method described in 2.8.1.

5.2.5. Measurement of anions in intact plant

Chloride, nitrate and phosphate were measured according to the methods described in 2,8.5, 2.8.6 and 2.8.7 respectively.

5.3. Results

5.3.1. The effect of ABA on the accumulation of anions in intact rice seedlings

In the root of intact rice seedlings, 10^{-7} M ABA did not show any significant effect on Cl^- accumulation except an inhibition at 6 hours of treatment (Fig. 31a). ABA, at 10^{-6} M, caused an increase in Cl^- accumulation by 19.6 to 8.0% at 24 to 48 hours of treatment after an initial inhibition from 3 to 6 hours of treatment (Fig. 31a). At the concentration of 10^{-5} M, ABA stimulated Cl^- accumulation by 8.0 to 9.3% at 3 to 48 hours of treatment in the root of intact rice seedlings (Fig. 31a).

In the shoot of intact rice seedlings, 10^{-7} M ABA caused an increase in Cl^- accumulation by 17.4 to 26.0% at 6 to 24 hours of treatment. However, accumulation of Cl^- in the shoot was decreased at 48 hours of treatment (Fig. 31b). Similarly, 10^{-6} M

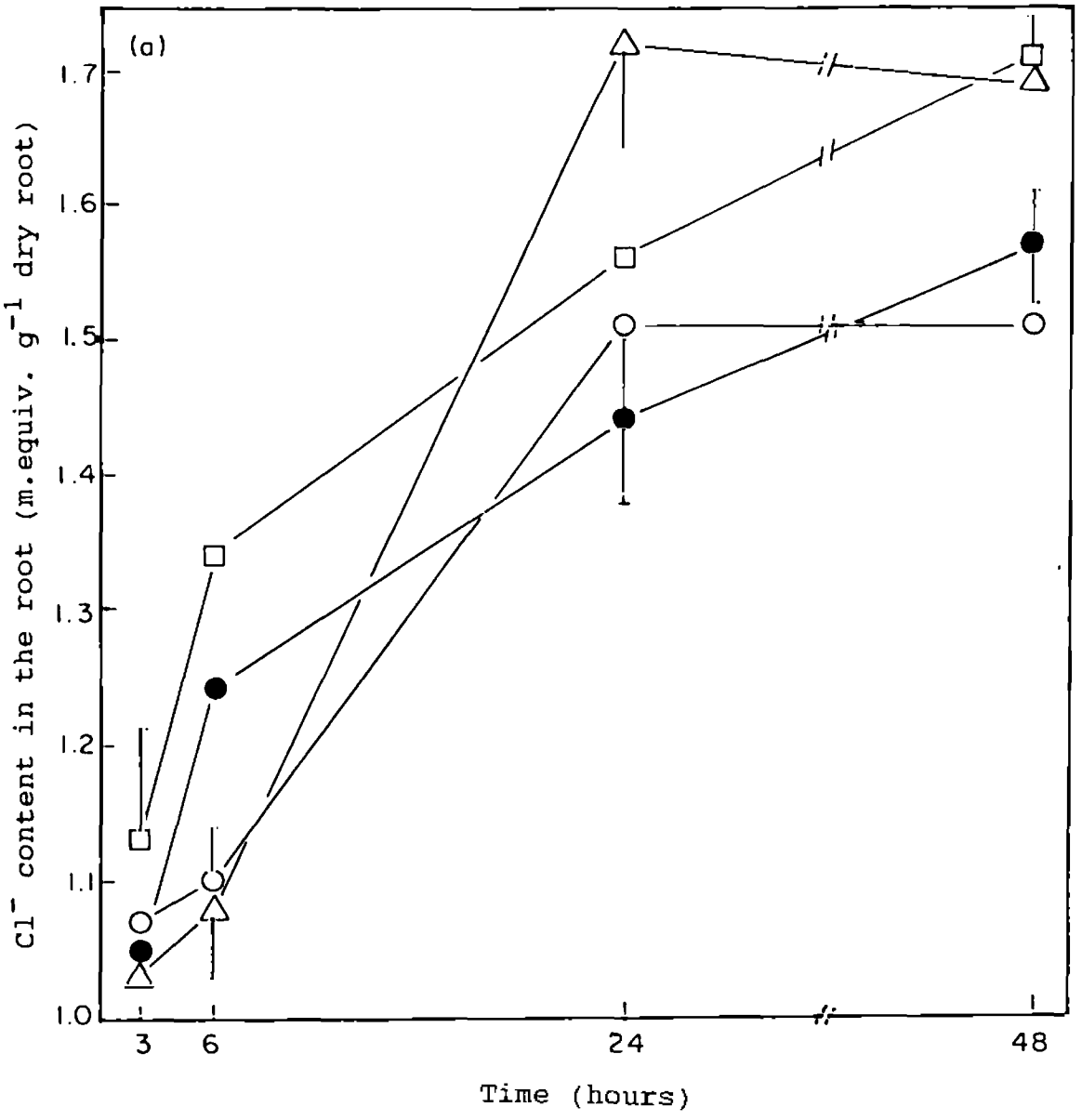

Fig. 31a. The effect of different concentrations of ABA on Cl^- accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 11.

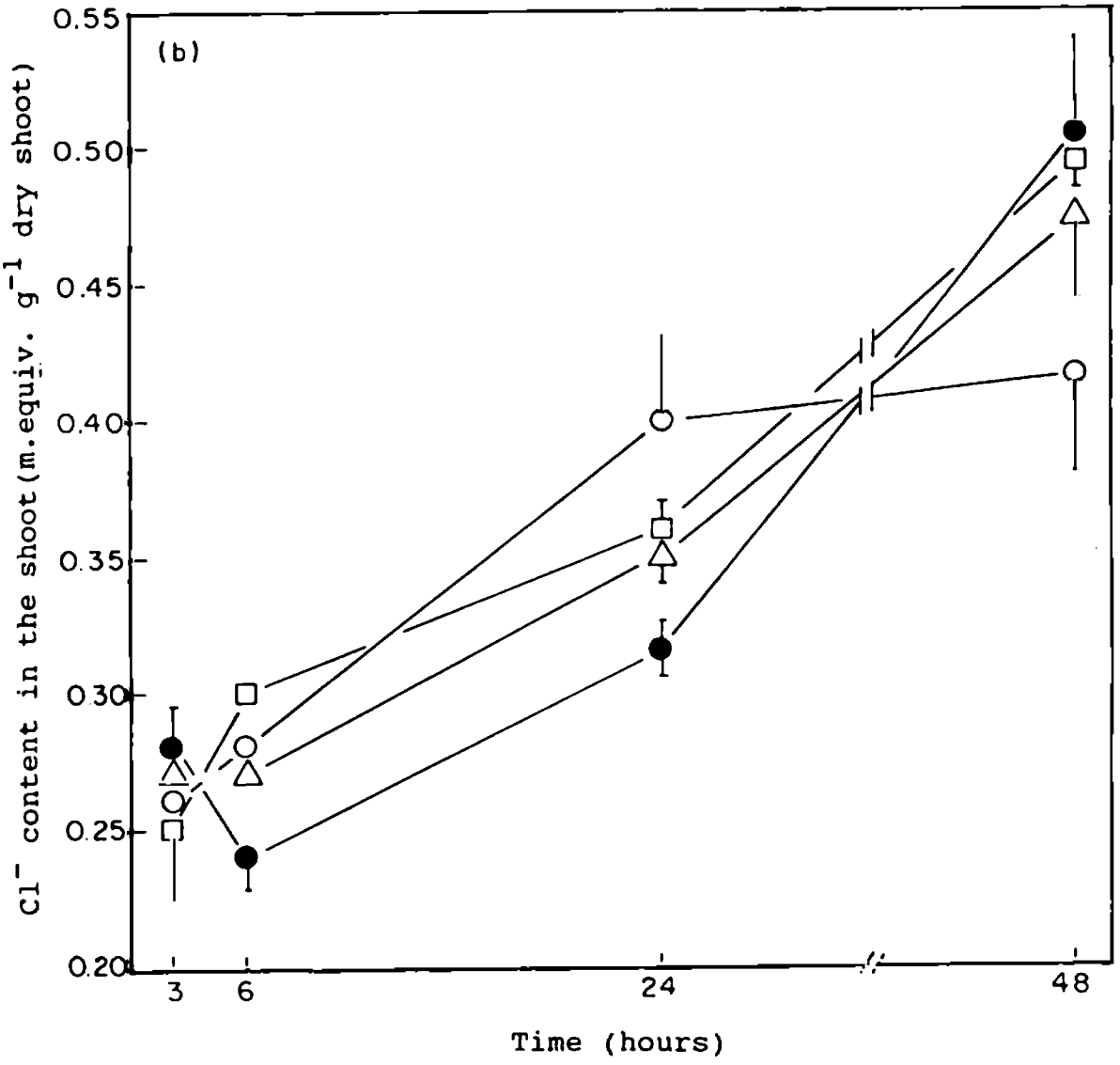

Fig. 31b. The effect of different concentrations of ABA on Cl^- accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as **Fig. 11.**

ABA increased Cl^- accumulation by 13.1 to 10.7 at 6 to 24 hours of treatment and the accumulation of Cl^- was decreased at 48 hours of treatment (Fig.31b). At the concentration of 10^{-5} M, ABA increased Cl^- accumulation by 25.9 to 14.9% at 6 to 24 hours of treatment after an initial decrease at 3 hours of treatment and the accumulation of Cl^- was levelled with the control at 48 hours of treatment in the shoot of intact rice seedlings (Fig. 31b).

In the root of intact rice seedlings, 10^{-7} M ABA caused an stimulation of NO_3^- accumulation by 60.2%, 2.2-fold and 96% at 6, 24 and 48 hours of treatment respectively (Fig. 32a). ABA, at 10^{-6} M, increased NO_3^- accumulation by 47.9% at 48 hours of treatment but did not show any significant effect at 6 and 24 hours of treatment (Fig. 32a). At the concentration of 10^{-5} M, ABA caused an increase in NO_3^- accumulation by 2.5-fold, 87.4 and 71.7% at 6, 24 and 48 hours of treatment respectively in the root of intact rice seedlings (Fig. 32a).

In the shoot of intact rice seedlings, 10^{-7} M ABA inhibited NO_3^- accumulation by 13.9 to 18.3% at 6 to 24 hours of treatment and the accumulation of NO_3^- was levelled with the control at 48 hours of treatment (Fig. 32b). ABA, at 10^{-6} M, also increased NO_3^- accumulation by 11.5% at 24 hours of treatment. The inhibitory effect declined gradually and the accumulation of NO_3^- was levelled with the control at 48 hours of treatment (Fig. 32b). At the concentration of 10^{-5} M, ABA caused a decrease in NO_3^- accumulation by 31.7 to 8.1% at 6 to 48 hours of treatment in the shoot of intact seedlings (Fig. 32b).

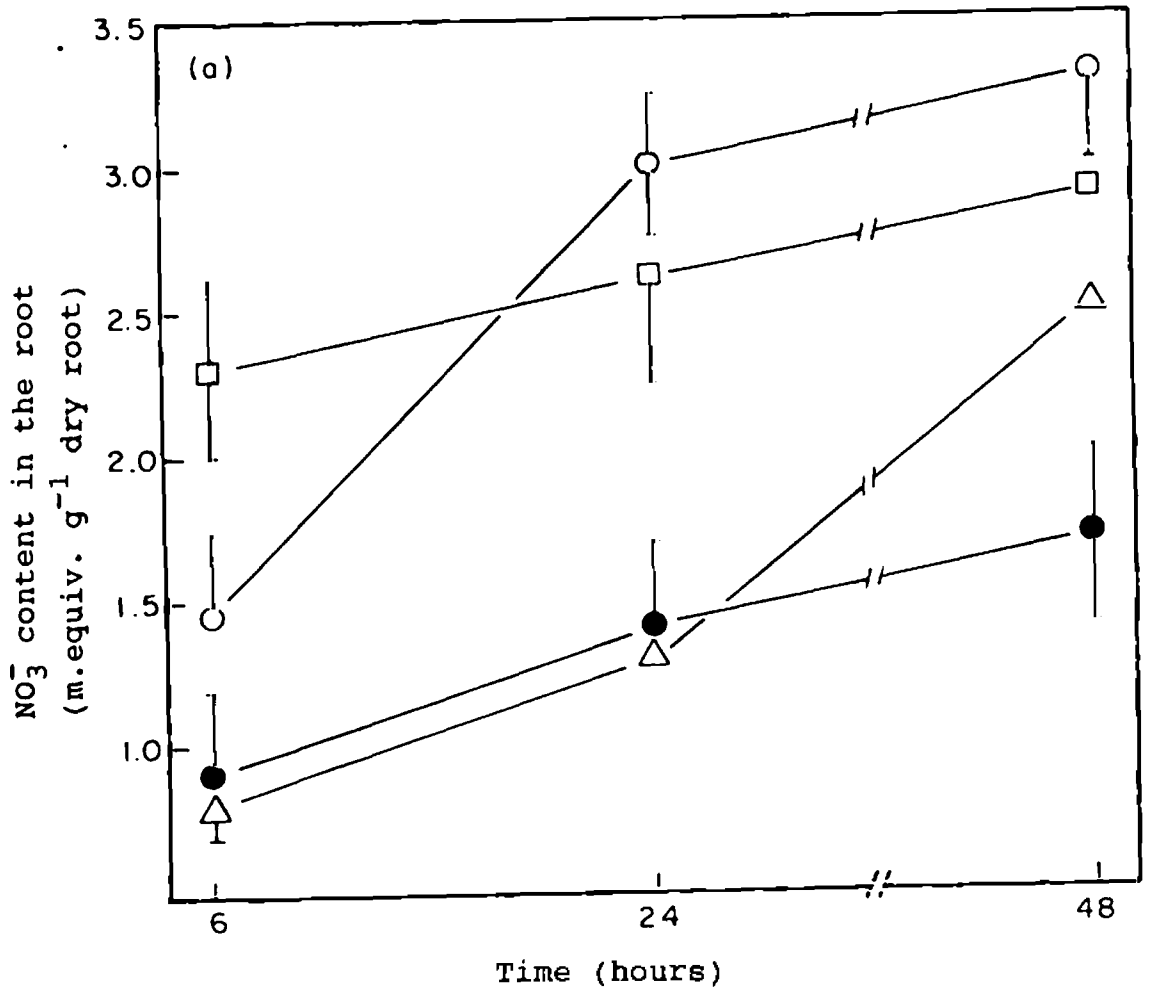

Fig. 32a. The effect of different concentrations of ABA on NO_3^- accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 11.

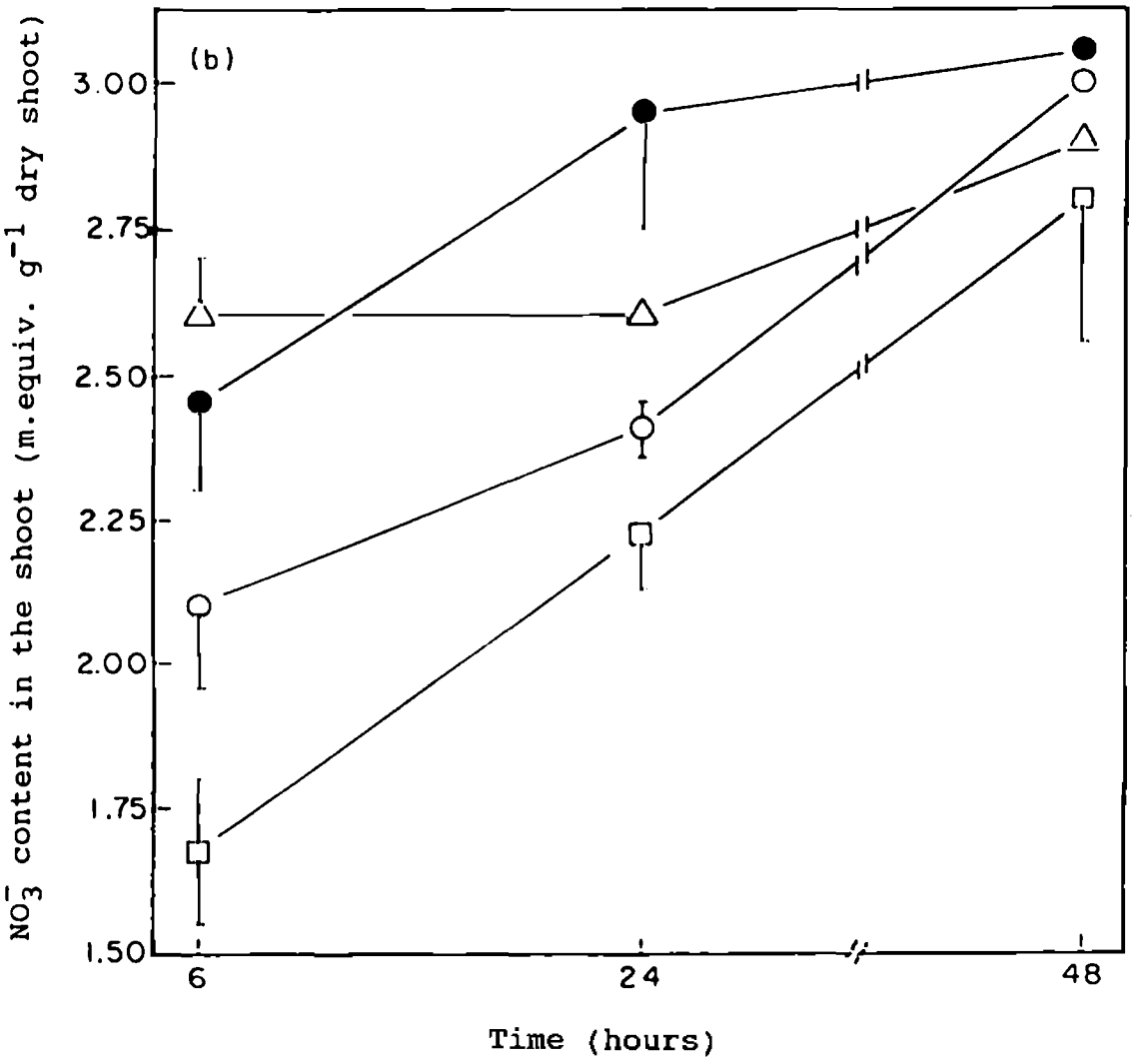

Fig. 32b. The effect of different concentrations of ABA on NO_3^- accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 11.

In the root of intact rice seedlings, 10^{-7} M ABA inhibited phosphate accumulation by 17.0 to 20.8% at 3 to 24 hours of treatment. The inhibitory effect gradually declined and the accumulation was increased by 21.5% at 48 hours of treatment (Fig. 33a). 10^{-6} M ABA decreased phosphate accumulation by 57.4 to 19.1% at 3 to 48 hours of treatment (Fig. 33a). ABA, at 10^{-5} M, also decreased phosphate accumulation in intact root of rice seedlings by 38.5 to 30.3% at 3 to 6 hours of treatment. The inhibitory effect declined gradually from 6 to 24 hours of treatment and ultimately led to an increase in phosphate accumulation by 11.0% at 48 hours of treatment (Fig. 33a).

In the shoot of intact rice seedlings, 10^{-7} M ABA stimulated phosphate accumulation by 47.4% at 48 hours of treatment but did not show any significant effect up to 24 hours of treatment (Fig. 33b). On the other hand, 10^{-6} M ABA decreased phosphate accumulation by 46.4 to 14.7% from 3 to 24 hours of treatment. The inhibitory effect gradually declined after 24 hours of treatment leading to a stimulation of 34.4% at 48 hours of treatment (Fig. 33b). ABA, at 10^{-5} M, showed a similar effect to that of 10^{-6} M ABA on phosphate accumulation. In that case, the inhibition of phosphate accumulation was 27.9 to 28.8% at 3 to 24 hours of treatment (Fig. 33b).

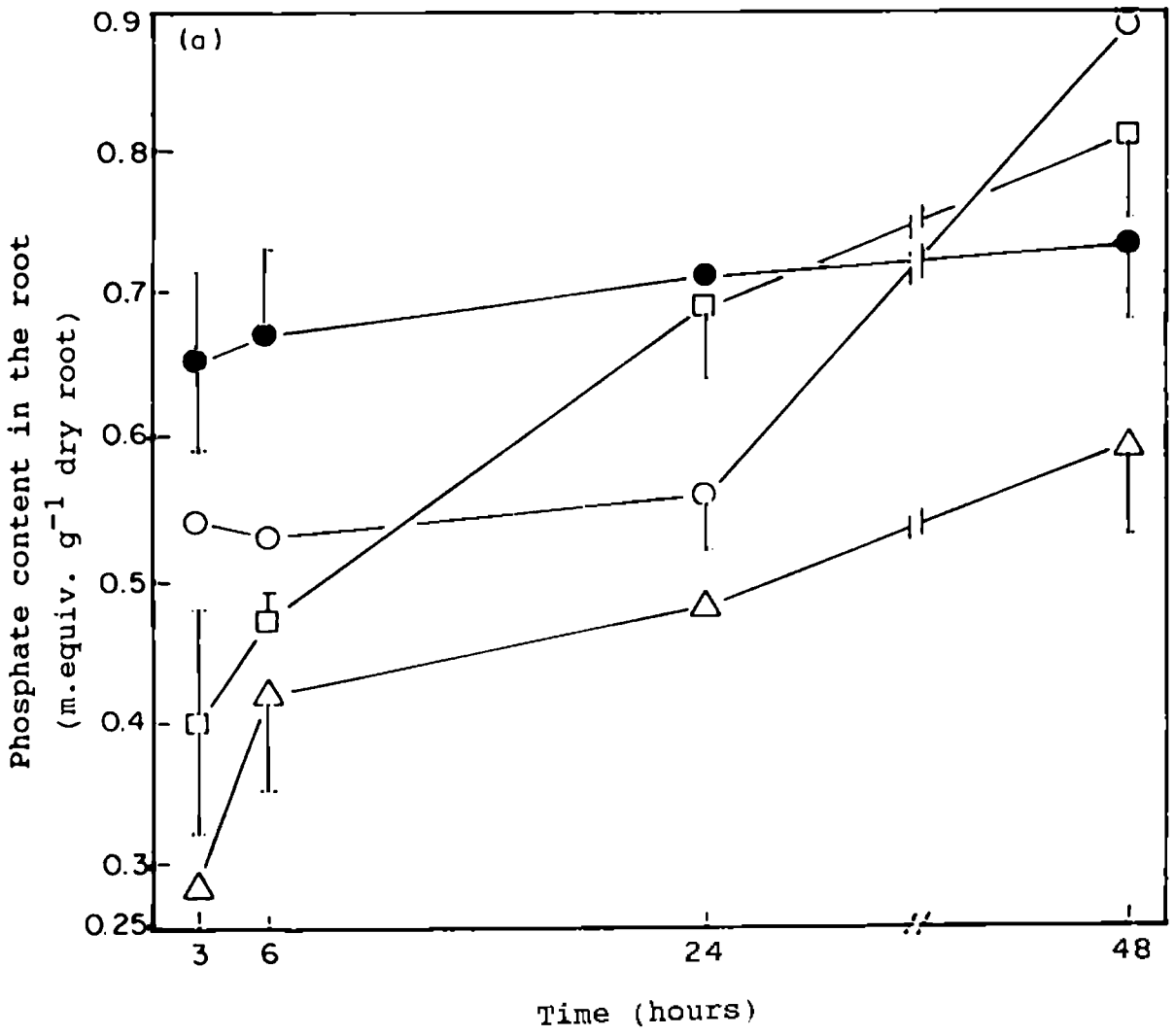

Fig. 33a. The effect of different concentrations of ABA on phosphate accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 11.

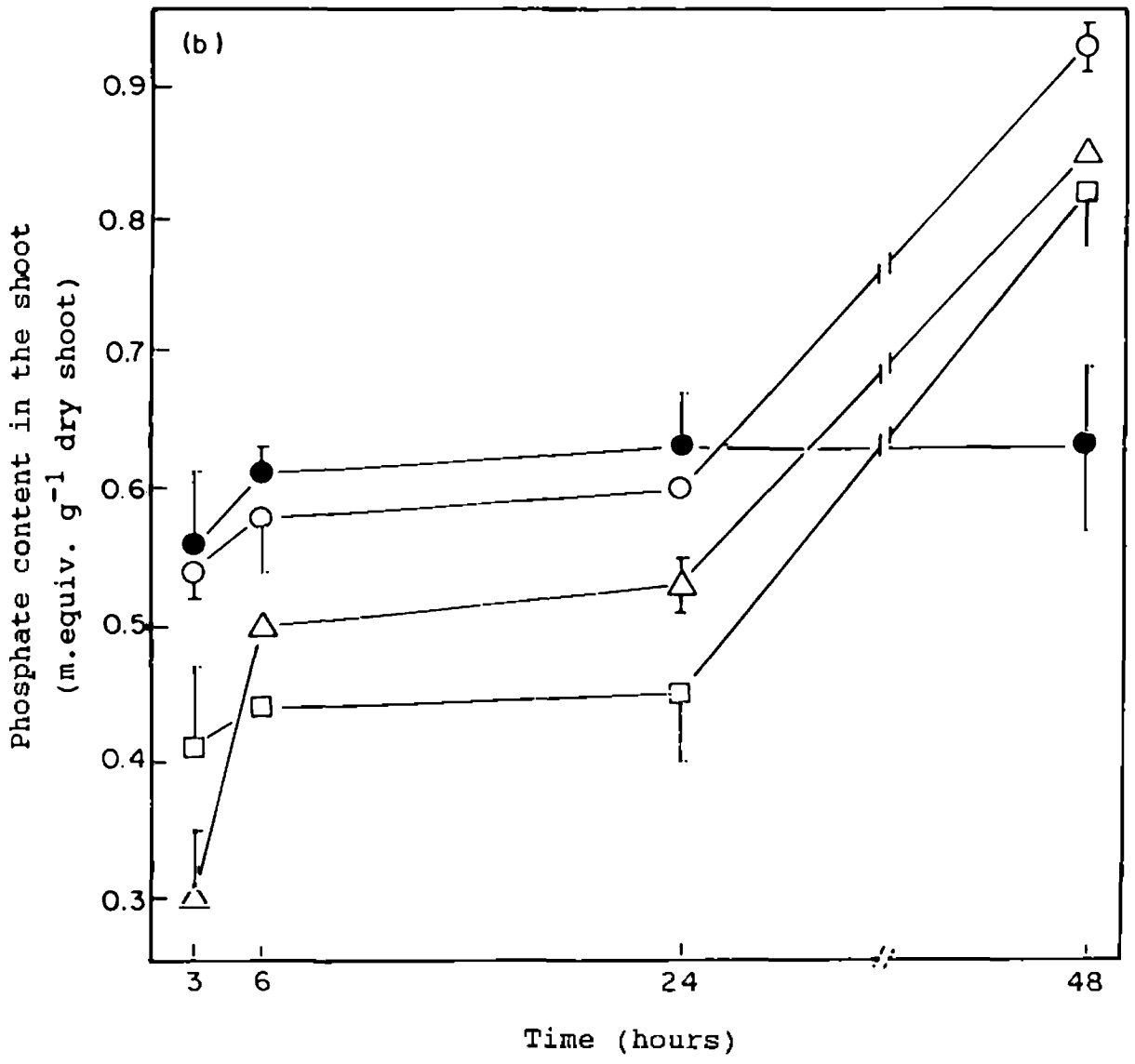

Fig. 33b. The effect of different concentrations of ABA on phosphate accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 11.

5.3.2. The effect of ABA on net influx and long distance transport of anions in intact rice seedlings

In intact rice seedlings, 10^{-7} M ABA increased the net influx ($\bar{\gamma}_{oc}$) of Cl^- by 13.3% at 6 hours of treatment after an initial decrease by 29.5% at 3 hours of treatment (Table 12). Similarly, 10^{-6} M ABA stimulated net influx of Cl^- by 13.3% at 6 hours of treatment after an initial decrease by 16.6% at 3 hours of treatment (Table 12). ABA, at 10^{-5} M, also stimulated net influx of Cl^- by 16.6% at 6 hours of treatment after an initial decrease by 11.9% at 3 hours of treatment (Table 12).

ABA, at 10^{-7} M, decreased long distance transport ($\bar{\gamma}_{cx}$) of Cl^- in intact seedlings by 42.8 and 27.9% at 3 and 48 hours of treatment respectively but increased by 12.5% at 6 to 24 hours of treatment (Table 12). On the other hand, 10^{-6} M ABA stimulated long distance transport of Cl^- by 12.5 to 20.0% at 6 to 48 hours after an initial inhibition by 35.7% at 3 hours of treatment (Table 12). Similarly, 10^{-5} M ABA increased long distance transport of Cl^- by 12.5 to 6.2% at 6 to 24 hours of treatment after an initial decrease by 42.8% at 3 hours of treatment in intact rice seedlings (Table 12).

ABA (10^{-7} M) decreased transport index of Cl^- at 3 to 6 hours of treatment. On the other hand, it increased transport index of Cl^- at 24 hours of treatment but levelled with the control at 48 hours of treatment (Table 12). 10^{-6} M ABA decreased transport index of Cl^- at 3 to 48 hours of treatment (Table 12). At the concentration of 10^{-5} M, ABA also decreased transport index of

Table 12. The effect of ABA on net influx and long distance transport of Cl^- in intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Table 2.

Time (hr)	Transport of Cl^- from root to shoot (γ_{cx}) (mg/shoot)				Net influx of Cl^- (γ_{oc}) (mg/plant)				Transport index $= (\frac{\gamma_{cx}}{\gamma_{oc}} \times 100)$			
	Control	ABA			Control	ABA			Control	ABA		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	3.313 ±0.854	1.893 ±0.236	2.130 ±0.410	1.893 ±0.236	4.970 ±0.710	3.550 ±0.410	4.141 ±0.720	4.378 ±0.626	66.65	53.32	51.43	43.23
0-6	1.893 ±0.236	2.130 ±0.410	2.130 ±0.410	2.130 ±0.000	3.550 ±0.205	4.023 ±0.313	4.023 ±0.236	4.141 ±0.313	53.32	52.94	52.94	51.43
0-24	1.893 ±0.118	2.130 ±0.205	1.893 ±0.118	2.011 ±0.118	4.970 ±0.894	4.970 ±0.355	5.325 ±1.248	4.260 ±0.205	38.08	42.85	35.54	47.20
0-48	2.958 ±0.829	2.133 ±0.358	2.366 ±0.118	2.728 ±0.121	5.088 ±1.053	3.790 ±0.430	4.378 ±0.118	5.098 ±0.319	58.13	56.27	54.04	53.51

Cl^- at 3, 6 and 48 hours of treatment except at 24 hours of treatment in intact rice seedlings (Table 12).

In intact rice seedlings, 10^{-7} M ABA inhibited net influx (Ψ_{oc}) of NO_3^- by 18.3 to 17.6% at 6 to 24 hours of treatment and the inhibitory effect was maintained up to 48 hours of treatment (Table 13). 10^{-6} M ABA also decreased net influx of NO_3^- by 18.4 to 16.3% at 24 to 48 hours of treatment (Table 13). At the concentration of 10^{-5} M, ABA also inhibited net influx of NO_3^- by 26.6 to 10.1% at 6 to 48 hours of treatment (Table 13).

ABA, at 10^{-7} M, inhibited long distance transport (Ψ_{cx}) of NO_3^- by 18.9, 28.5 and 12.2% at 6, 24 and 48 hours of treatment respectively in intact seedlings (Table 13). At the concentration of 10^{-6} M, ABA decreased long distance transport of NO_3^- by 18.4 to 22.2% at 24 to 48 hours of treatment (Table 13). 10^{-5} M ABA also inhibited long distance transport of NO_3^- by 40.5 to 18.5% at 6 to 48 hours of treatment in intact seedlings (Table 13).

ABA (10^{-7}, 10^{-6} and 10^{-5} M) decreased transport index of No_3^- at 6 to 48 hours of treatment in intact rice seedlings (Table 13).

In intact seedlings, 10^{-7} M ABA increased net influx (Ψ_{oc}) of phosphate by 54.0% at 48 hours of treatment but decreased that by 34.2% at 24 hours of treatment (Table 14). On the other hand, 10^{-6} M ABA decreased net influx of phosphate by 43.5 and 34.2% at 3 and 24 hours of treatment but increased that at 74.3% at 48 hours of treatment (Table 14). At the concentration of 10^{-5} M,

Table 13. The effect of ABA on net influx and long distance transport of NO_3^- in intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Table 2.

Time (hr)	Transport of NO_3^- from root to shoot (γ_{cx}) (mg/shoot)				Net influx of No_3^- (γ_{oc}) (mg/plant)				Transport index $\frac{\gamma_{cx}}{\gamma_{oc}} \times 100$			
	Control	ABA			Control	ABA			Control	ABA		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-6	1.233 ±0.218	1.000 ±0.104	1.273 ±0.193	0.733 ±0.066	1.310 ±0.236	1.070 ±0.104	1.360 ±0.195	0.961 ±0.215	94.12	93.45	93.60	76.27
0-24	1.516 ±0.169	1.083 ±0.033	1.236 ±0.043	1.050 ±0.000	1.680 ±0.285	1.383 ±0.143	1.370 ±0.010	1.343 ±0.162	90.23	78.30	90.21	78.18
0-48	1.633 ±0.133	1.433 ±0.183	1.270 ±0.040	1.330 ±0.108	1.816 ±0.136	1.783 ±0.361	1.520 ±0.203	1.636 ±0.109	89.92	80.37	83.55	81.29

Table 14. The effect of ABA on net influx and long distance transport of phosphate in intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Table 2.

Time (hr)	Transport of phosphate from root to shoot (γ_{cx}) (mg/shoot)				Net influx of phosphate (γ_{oc}) (mg/plant)				Transport index $= (\frac{\gamma_{cx}}{\gamma_{oc}} \times 100)$			
	Control	ABA			Control	ABA			Control	ABA		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.153 ±0.022	0.152 ±0.008	0.088 ±0.028	0.112 ±0.021	0.186 ±0.021	0.195 ±0.004	0.105 ±0.034	0.129 ±0.029	82.25	77.94	83.80	86.82
0-6	0.161 ±0.017	0.162 ±0.031	0.156 ±0.046	0.105 ±0.020	0.194 ±0.022	0.180 ±0.036	0.178 ±0.049	0.133 ±0.020	82.98	90.00	87.64	78.94
0-24	0.072 ±0.024	0.041 ±0.029	0.041 ±0.029	0.012 ±0.000	0.105 ±0.030	0.069 ±0.029	0.069 ±0.029	0.045 ±0.005	68.57	59.42	59.42	26.66
0-48	0.041 ±0.029	0.106 ±0.006	0.106 ±0.006	0.090 ±0.009	0.074 ±0.027	0.114 ±0.029	0.129 ±0.010	0.128 ±0.016	55.40	92.98	82.17	70.31

ABA inhibited net influx of phosphate by 30.6 to 57.1% at 3 to 24 hours of treatment but stimulated by 72.9% at 48 hours of treatment (Table 14).

ABA (10^{-7}, 10^{-6} and 10^{-5} M) inhibited long distance transport (Ψ_{CX}) of phosphate in intact seedlings from 3 to 24 hours of treatment. The inhibitory effect was nullified leading to a stimulation of long distance transport of phosphate over the next 24 hours i.e. from 24 to 48 hours of treatment (Table 14).

In intact rice seedlings, 10^{-7} M increased transport index of phosphate at 6 and 48 hours of treatment but decreased that at 3 and 24 hours of treatment (Table 14). ABA, at 10^{-6} M, increased transport index of phosphate at 3 to 48 hours of treatment except at 24 hours of treatment (Table 4). At the concentration of 10^{-5} M, ABA also increased transport index of phosphate at 3 and 48 hours of treatment but decreased that at 6 to 24 hours of treatment in intact rice seedlings (Table 14).

5.3.3. The effect of kinetin on the accumulation of anions in intact rice seedlings

In the root of intact rice seedlings, 10^{-7} M kinetin inhibited Cl^- accumulation by 7.3 to 9.4% at 6 to 24 hours of treatment. The inhibitory effect gradually declined and levelled with the control at 48 hours of treatment (Fig. 34a). 10^{-6} M kinetin also decreased Cl^- accumulation by 8.8 to 6.2% at 3 to 48 hours of treatment (Fig. 34a). Kinetin, at the concentration of 10^{-5} M, increased Cl^- accumulation by 7.5 to 10.9% at 6 to 48 hours of

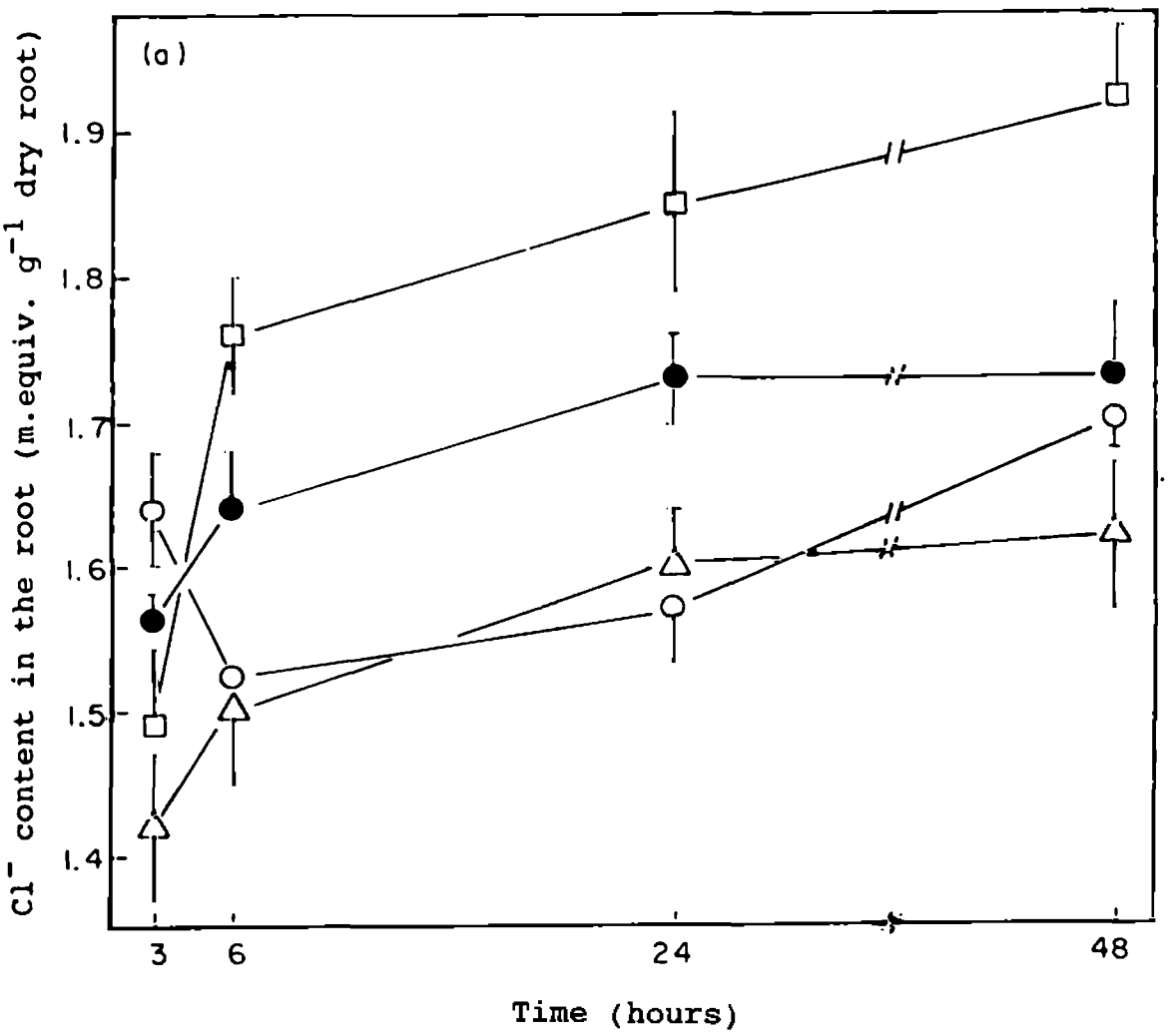

Fig. 34a. The effect of different concentrations of kinetin on Cl^- accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

treatment in the root of intact rice seedlings after an initial decrease at 3 hours of treatment (Fig. 34a).

In the shoot of intact rice seedlings, 10^{-7} M kinetin decreased Cl^- accumulation at 6 to 24 hours of treatment. The inhibitory effect was declined leading to an increase in Cl^- accumulation at 48 hours of treatment (Fig. 34b). Kinetin, at 10^{-6} M, caused an increase in Cl^- accumulation by 11.3 to 15.6% at 24 to 48 hours of treatment (Fig. 34b). Similarly, 10^{-5} M kinetin increased Cl^- accumulation at 8.7 to 11.6% at 24 to 48 hours of treatment in the shoot of intact seedlings (Fig. 34b).

In the root of intact rice seedlings, 10^{-7} M kinetin caused a decrease in NO_3^- accumulation by 46.1% at 6 hours of treatment and the inhibitory effect was maintained up to 48 hours of treatment (Fig. 35a). 10^{-6} M kinetin also decreased NO_3^- accumulation by 37.0, 17.1 and 32.4% at 6, 24 and 48 hours of treatment respectively (Fig. 35a). On the other hand, 10^{-5} M kinetin increased NO_3^- accumulation by 15.0, 22.9 and 16.3% at 6, 24 and 48 hours of treatment respectively in the root of intact seedlings (Fig. 35a).

In the shoot of intact rice seedlings, 10^{-7} M kinetin gradually increased NO_3^- accumulation by 11.7 to 91.4% over a period of 6 to 48 hours of treatment (Fig.35b). 10^{-6} M kinetin did not show any significant effect on NO_3^- accumulation in the shoot of intact seedlings (Fig. 35b). In the shoot, kinetin, at 10^{-5} M, caused 2.0- 2.5- and 2.2-fold increase at 6, 24 and 48 hours of treatment respectively (Fig. 35b).

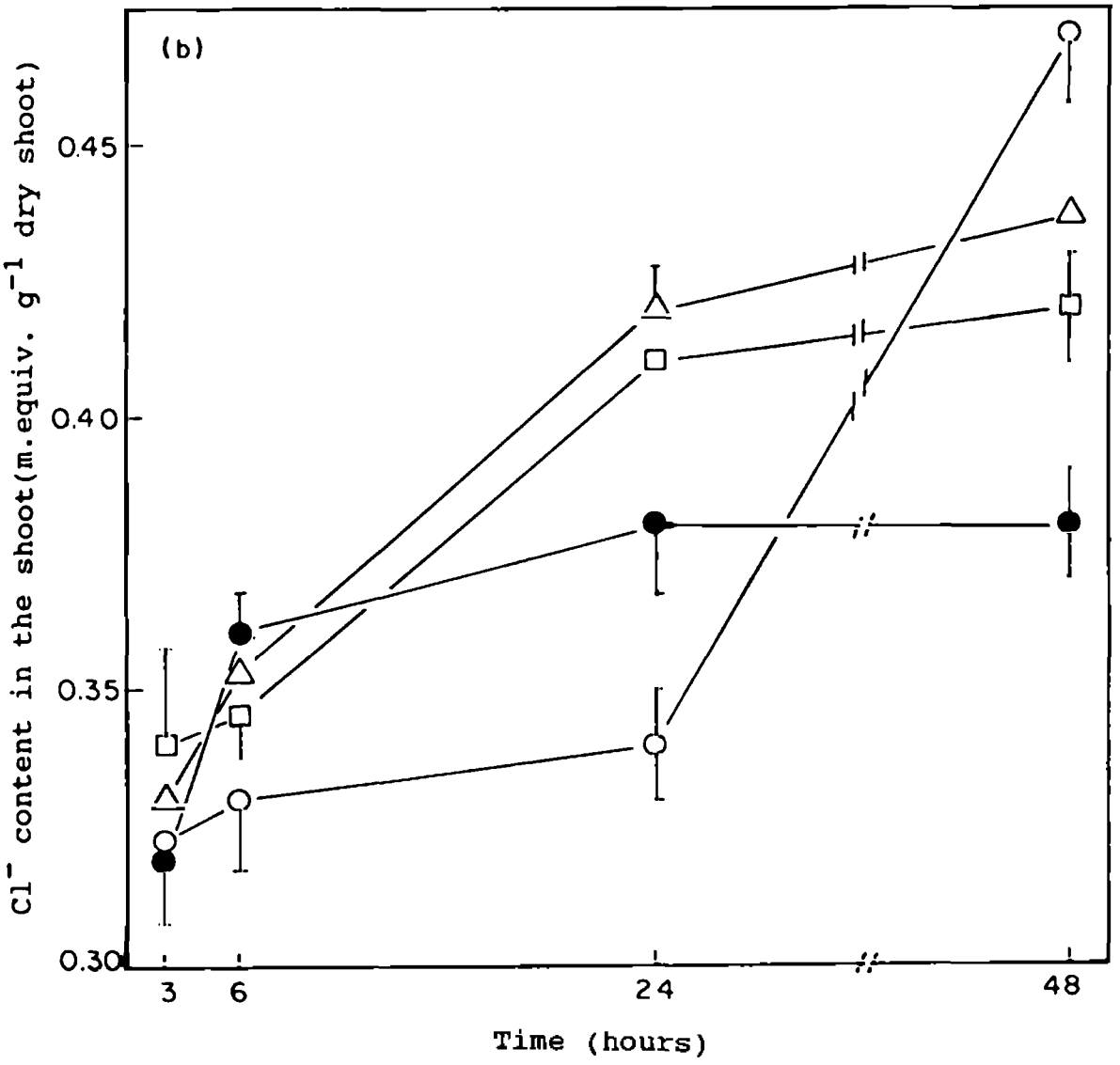

Fig. 34b. The effect of different concentrations of kinetin on Cl^- accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

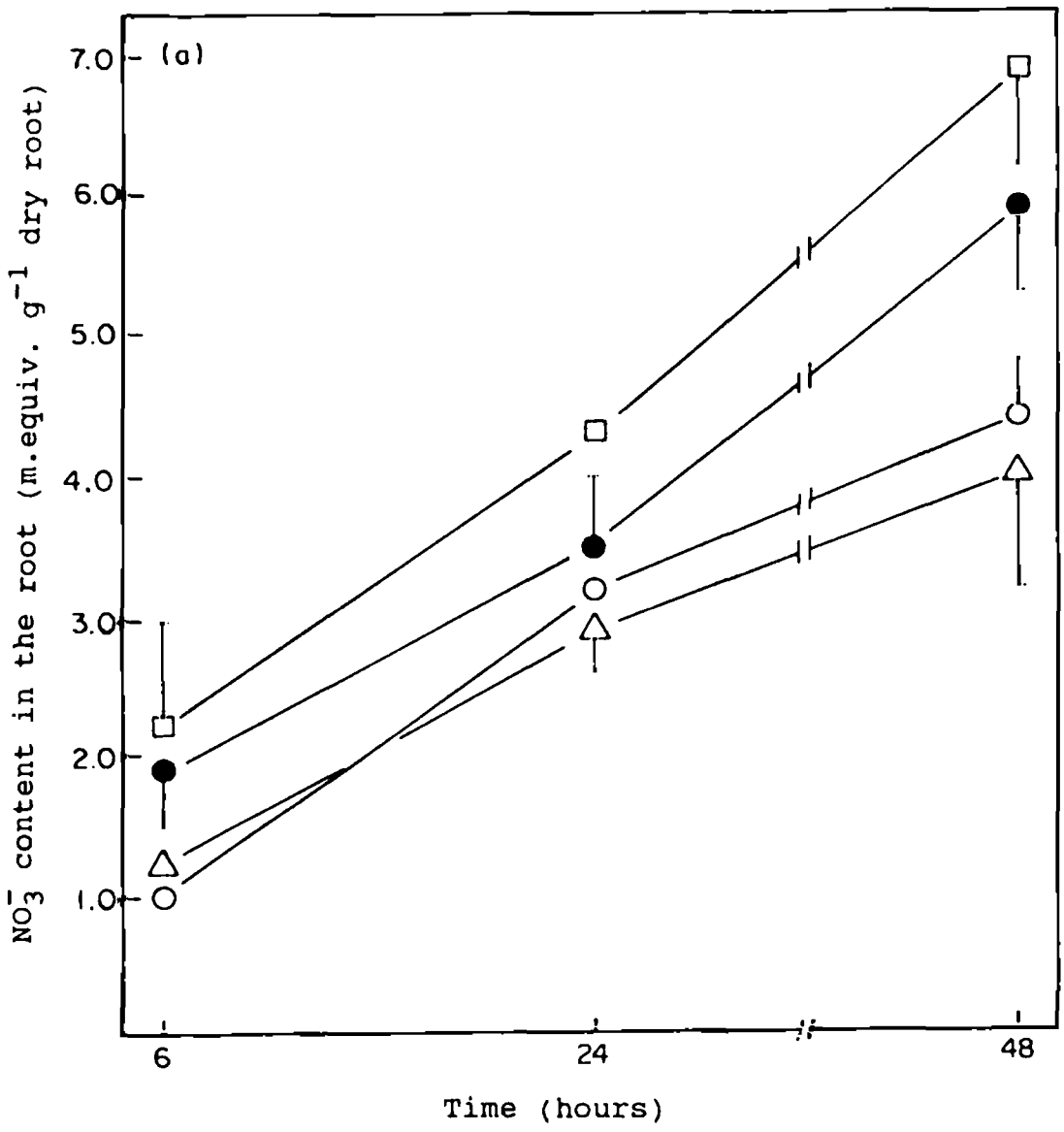

Fig. 35a. The effect of different concentrations of kinetin on NO_3^- accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

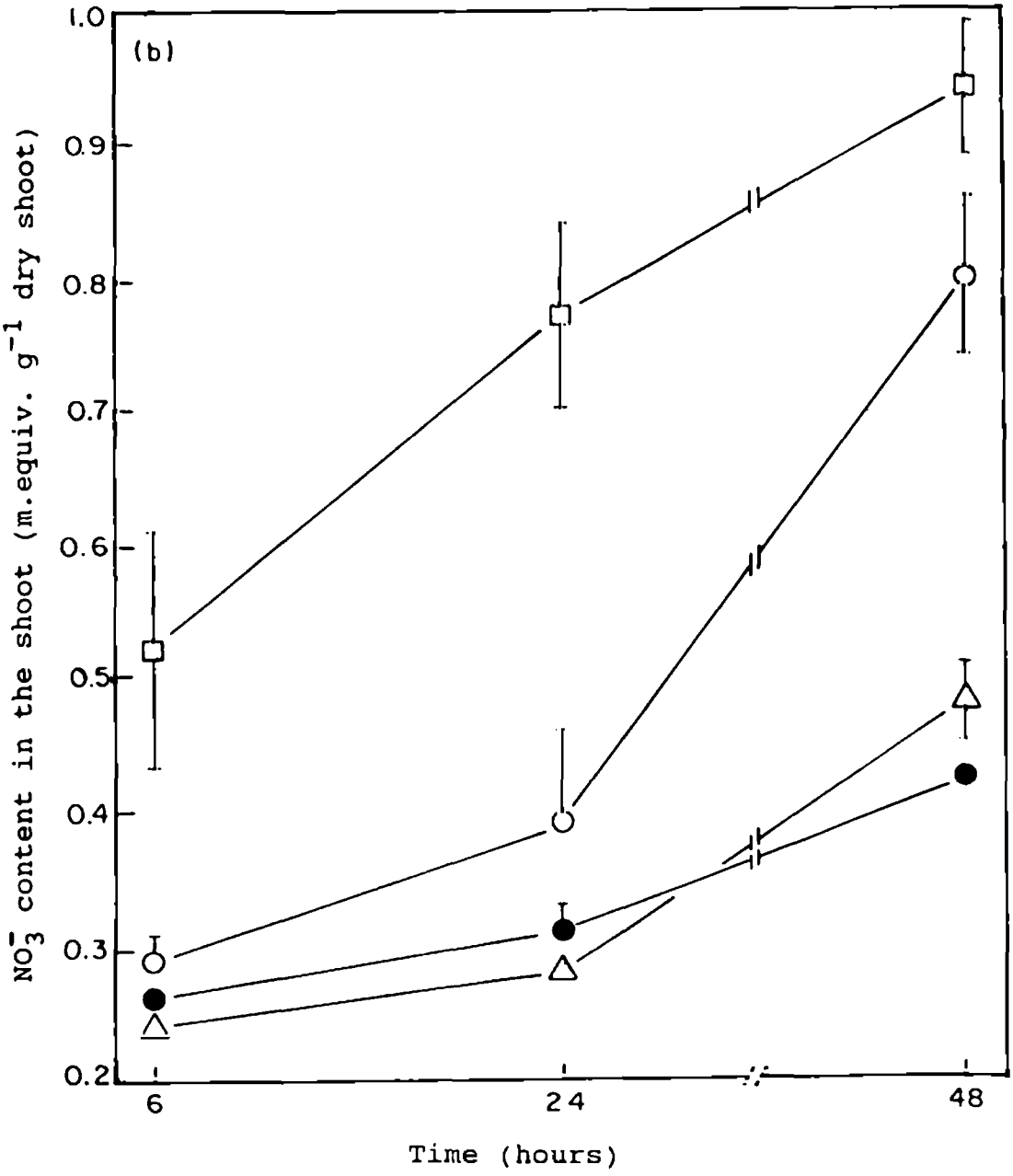

Fig. 35b. The effect of different concentrations of kinetin on NO_3^- accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

In the root of intact rice seedlings, 10^{-7} M kinetin increased phosphate accumulation by 24.7, 6.6 and 19.6% at 6, 24 and 48 hours of treatment respectively after an initial decrease by 16.5% at 3 hours of treatment (Fig. 36a). 10^{-6} M kinetin also increased phosphate accumulation by 6.4 to 13.1% at 6 to 48 hours of treatment after an initial inhibition by 8.1% at 3 hours of treatment (Fig. 36a). At the concentration of 10^{-5} M, kinetin did not show any significant effect on phosphate accumulation at 24 and 48 hours of treatment (Fig. 36a).

In the shoot of intact rice seedlings, 10^{-7} M kinetin stimulated phosphate accumulation by 24.9 to 48.8% at 3 to 24 hours of treatment and the stimulatory effect was maintained up to 48 hours of treatment (Fig. 36b). Similarly, 10^{-6} M kinetin stimulated phosphate accumulation by 21.2 to 60.9% at 3 to 6 hours of treatment and the stimulatory effect was maintained up to 48 hours of treatment (Fig. 36b). On the other hand, 10^{-5} M kinetin did not show any significant effect on phosphate accumulation in the shoot of intact seedlings at 24 and 48 hours of treatment (Fig. 36b).

5.3.4. The effect of kinetin on net influx and long distance transport of anions in intact rice seedlings

In intact seedlings, 10^{-7} M kinetin inhibited net influx (Ψ_{oc}) of Cl^- by 14.0 to 12.8% at 6 to 24 hours of treatment. The inhibitory effect was nullified leading to a stimulation of 36.7% at 48 hours of treatment (Table 15). Similarly, 10^{-6} M kinetin

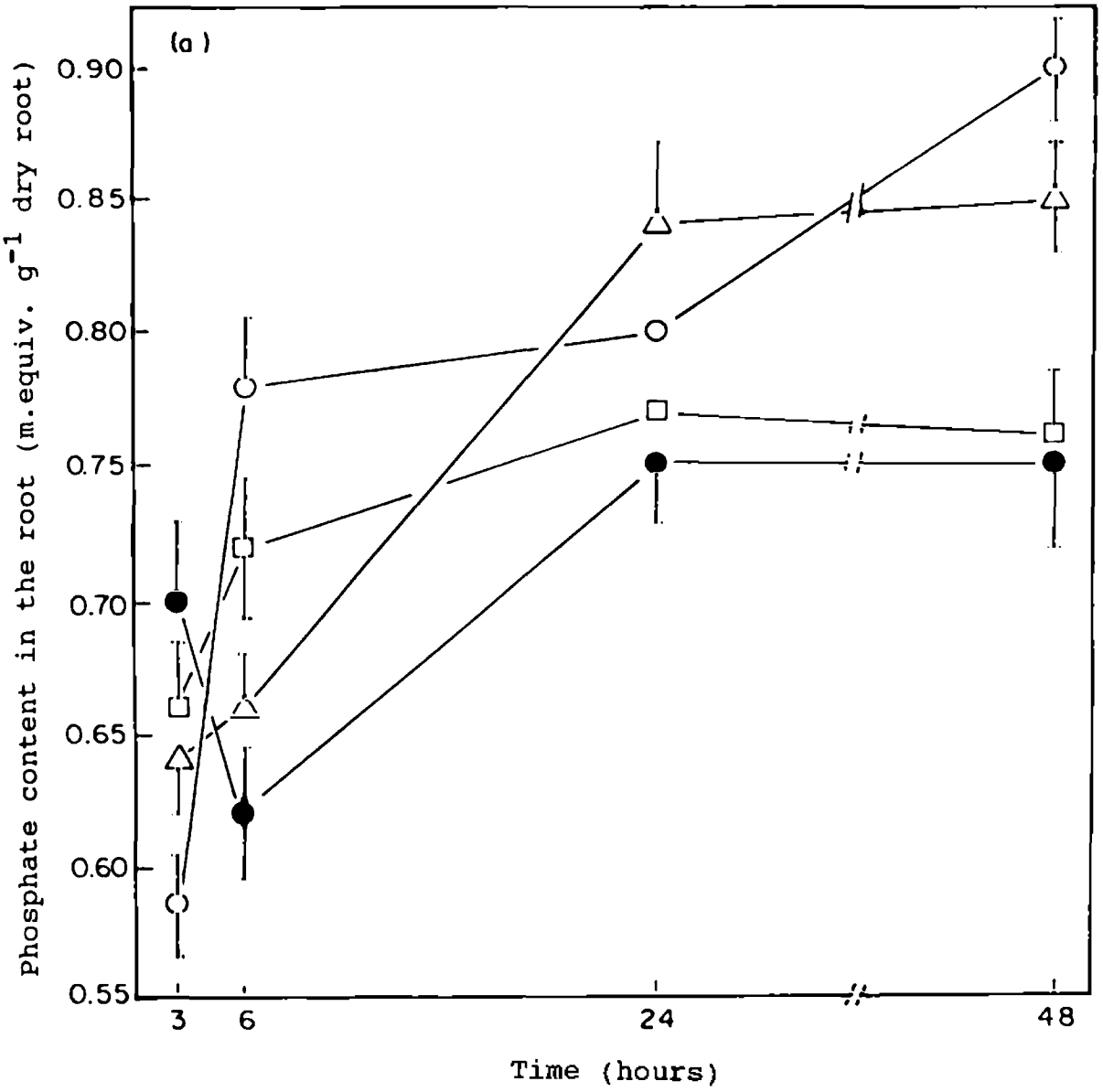

Fig. 36a. The effect of different concentrations of kinetin on phosphate accumulation in the root of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

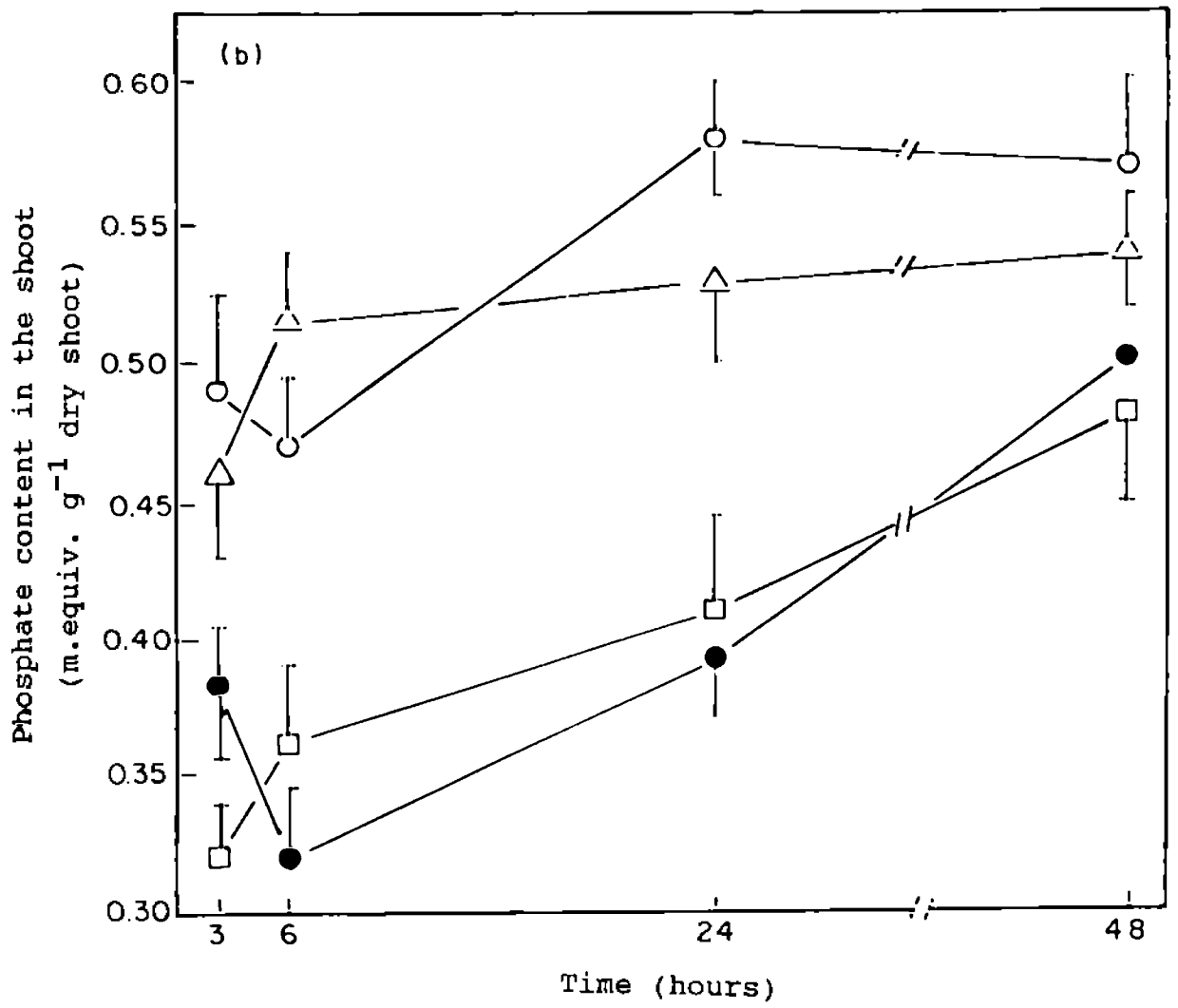

Fig. 36b. The effect of different concentrations of kinetin on phosphate accumulation in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Fig. 16.

inhibited net influx of Cl^- by 9.4 and 12.0% at 3 to 6 hours of treatment. The inhibitory effect was nullified leading to a stimulation of 19.5% at 48 hours of treatment (Table 15). kinetin, at 10^{-5} M, stimulated net influx of Cl^- by 19.5% at 48 hours of treatment in intact rice seedlings (Table 15).

Kinetin, at 10^{-7} M, decreased long distance transport (Ψ_{CX}) of Cl^- by 21.4 to 15.8% at 6 to 24 hours of treatment. The inhibitory effect was nullified leading to a stimulation of 38.9% at 48 hours of treatment (Table 15). 10^{-6} and 10^{-5} M kinetin decreased long distance transport of Cl^- by 14.2% at 6 hours of treatment while increased that by 12.8% at 48 hours of treatment (Table 15).

In intact seedlings, 10^{-7} M kinetin decreased transport index of Cl^- at 6 to 24 hours of treatment (Table 15). 10^{-6} M kinetin also decreased transport index of Cl^- at 6 to 48 hours of treatment after an initial increase at 3 hours of treatment (Table 15). On the other hand, 10^{-5} M kinetin increased transport index of Cl^- at 3 and 24 hours of treatment but decreased that at 6 and 48 hours of treatment in intact rice seedlings (Table 15).

In intact seedlings, 10^{-7} M kinetin increased net influx (Ψ_{OC}) of NO_3^- by 13.3 to 33.5% at 24 to 48 hours of treatment after an initial decrease by 19.7% at 6 hours of treatment (Table 16). 10^{-6} M kinetin decreased net influx of NO_3^- by 11.3% at 48 hours of treatment (Table 16). On the other hand, 10^{-5} M kinetin

Table 15. The effect of kinetin on net influx and long distance transport of Cl^- in intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Table 7.

Time (hr)	Transport of Cl^- from root to shoot (γ_{cx}) (mg/shoot)				Net influx of Cl^- (γ_{oc}) (mg/plant)				Transport index $\frac{\gamma_{cx}}{\gamma_{oc}} \times 100$			
	Control	Kinetin			Control	Kinetin			Control	Kinetin		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	2.360 ±0.236	2.360 ±0.236	2.360 ±0.236	2.600 ±0.236	4.970 ±0.205	4.970 ±0.205	4.500 ±0.427	5.210 ±0.312	47.48	47.48	52.44	49.90
0-6	3.310 +0.478	2.600 ±0.116	2.840 ±0.000	2.840 ±0.205	5.920 ±0.427	5.090 ±0.118	5.210 ±0.312	5.450 ±0.235	55.91	51.08	54.51	52.11
0-24	2.960 ±0.312	2.490 ±0.000	2.720 ±0.236	2.960 ±0.120	5.440 ±0.314	4.740 ±0.312	5.090 ±0.236	5.330 ±0.208	54.41	52.53	53.43	55.53
0-48	2.720 ±0.116	3.780 ±0.947	3.070 ±0.473	3.070 ±0.236	4.850 ±0.311	6.630 ±0.777	5.800 ±0.311	5.800 ±0.517	56.08	57.01	52.93	52.93

Table 16. The effect of kinetin on net influx and long distance transport of NO_3^- in intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Table 7.

Time (hr)	Transport of No_3^- from root to shoot (γ_{cx}) (mg/shoot)				Net influx of NO_3^- (γ_{oc}) (mg/plant)				Transport index $\frac{\gamma_{cx}}{\gamma_{oc}} \times 100$			
	Control	Kinetin			Control	Kinetin			Control	Kinetin		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-6	0.123 ±0.000	0.136 ±0.000	0.119 ±0.000	0.246 ±0.101	0.289 ±0.004	0.232 ±0.001	0.291 ±0.002	0.423 ±0.103	42.56	58.62	40.89	58.15
0-24	0.146 ±0.003	0.206 ±0.049	0.156 ±0.006	0.363 ±0.043	0.426 ±0.012	0.483 ±0.049	0.423 ±0.048	0.690 ±0.050	34.27	42.65	36.87	52.60
0-48	0.213 ±0.003	0.426 ±0.190	0.226 ±0.013	0.473 ±0.049	0.646 ±0.159	0.863 ±0.185	0.573 ±0.068	1.200 ±0.112	32.97	49.36	39.44	39.41

increased net influx of NO_3^- by 46.3 to 85.7% at 6 to 48 hours of treatment (Table 16).

Kinetin, at 10^{-7} M, caused 10.5- to 2.0-fold increase in long distance transport (Ψ_{cx}) of NO_3^- from 6 to 48 hours of treatment (Table 16). 10^{-6} M kinetin did not show any significant effect on long distance transport of NO_3^- in intact rice seedlings (Table 16). However, 10^{-5} M kinetin caused a 2-fold increase in long distance transport of NO_3^- at 6 hours of treatment and the stimulatory effect was maintained up to 48 hours of treatment (Table 16).

In intact rice seedlings, 10^{-7} M kinetin caused an increase in transport index of NO_3^- at 6 to 48 hours of treatment (Table 16). 10^{-6} M kinetin increased transport index of NO_3^- at 24 to 48 hours of treatment after an initial decrease at 6 hours of treatment (Table 16). Kinetin, at 10^{-5} M, also increased transport index of NO_3^- at 6 to 48 hours of treatment in intact rice seedlings (Table 16).

In intact seedlings, 10^{-7} M kinetin increased net influx (Ψ_{oc}) of phosphate by 43.5, 50.8 and 38.0% at 3, 6 and 24 hours of treatment respectively and the stimulatory effect was maintained up to 48 hours of treatment (Table 17). 10^{-6} M kinetin also increased net influx of phosphate by 36.7 to 49.2% at 3 to 24 hours of treatment (Table 17). Kinetin, at 10^{-5} M, increased net influx of phosphate by 13.6, 48.2, 12.6 and 17.3% at 3, 6, 24 and 48 hours of treatment respectively (Table 17).

Table 17. The effect of kinetin on net influx and long distance transport of phosphate in intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise as Table 7.

Time (hr)	Transport of phosphate from root to shoot (γ_{cx}) (mg/shoot)				Net influx of phosphate (γ_{oc}) (mg/plant)				Transport index $= (\frac{\gamma_{cx}}{\gamma_{oc}} \times 100)$			
	Control	Kinetin			Control	Kinetin			Control	Kinetin		
		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M		10^{-7} M	10^{-6} M	10^{-5} M
0-3	0.080 ±0.008	0.122 ±0.016	0.122 ±0.016	0.096 ±0.013	0.117 ±0.006	0.168 ±0.023	0.160 ±0.016	0.133 ±0.011	68.37	72.61	76.25	72.18
0-6	0.082 ±0.037	0.122 ±0.016	0.133 ±0.018	0.132 ±0.038	0.116 ±0.035	0.175 ±0.012	0.172 ±0.026	0.172 ±0.035	70.68	69.71	77.32	76.74
0-24	0.088 ±0.008	0.141 ±0.010	0.142 ±0.024	0.116 ±0.044	0.126 ±0.016	0.174 ±0.021	0.188 ±0.031	0.142 ±0.048	69.84	81.03	75.53	81.69
0-48	0.122 ±0.016	0.114 ±0.023	0.125 ±0.026	0.141 ±0.010	0.156 ±0.016	0.167 ±0.025	0.156 ±0.030	0.183 ±0.016	78.20	68.26	80.12	77.04

Kinetin, at 10^{-7} M, increased long distance transport (Ψ_{CX}) of phosphate in intact rice seedlings by 52.5, 48.7 and 60.2% at 3, 6 and 24 hours of treatment respectively (Table 17). Similarly, 10^{-6} M kinetin increased long distance transport of phosphate by 52.5, 62.1 and 61.3% at 3, 6 and 24 hours of treatment and the stimulatory effect was maintained up to 48 hours of treatment (Table 17). 10^{-5} M kinetin also increased long distance transport of phosphate by 20.0, 60.9, 31.8 and 15.5% at 3, 6, 24 and 48 hours of treatment respectively in intact seedlings (Table 17).

Transport index of phosphate was increased by 10^{-7} M kinetin at 3 and 24 hours of treatment but decreased that at 6 and 48 hours of treatment respectively (Table 17). 10^{-6} M kinetin also increased transport index of phosphate at 3 to 48 hours of treatment (Table 17). Kinetin, at 10^{-5} M, increased transport index of phosphate at 3 to 24 hours of treatment but decreased that at 48 hours of treatment in intact rice seedlings (Table 17).

5.3.5. The effect of ABA on the growth of intact rice seedlings

The root growth of intact rice seedlings was inhibited by 7.7, 14.2 and 6.6% by 10^{-7} M ABA at 3, 6 and 24 hours of treatment respectively (Fig. 37a). At the concentration of 10^{-6} M, ABA had no effect on the root growth at 6 to 24 hours of treatment (Fig. 37a). ABA at the concentration of 10^{-5} M decreased root growth by 7.7 to 6.2% at 3 to 48 hours of treatment in intact seedlings (Fig. 37a).

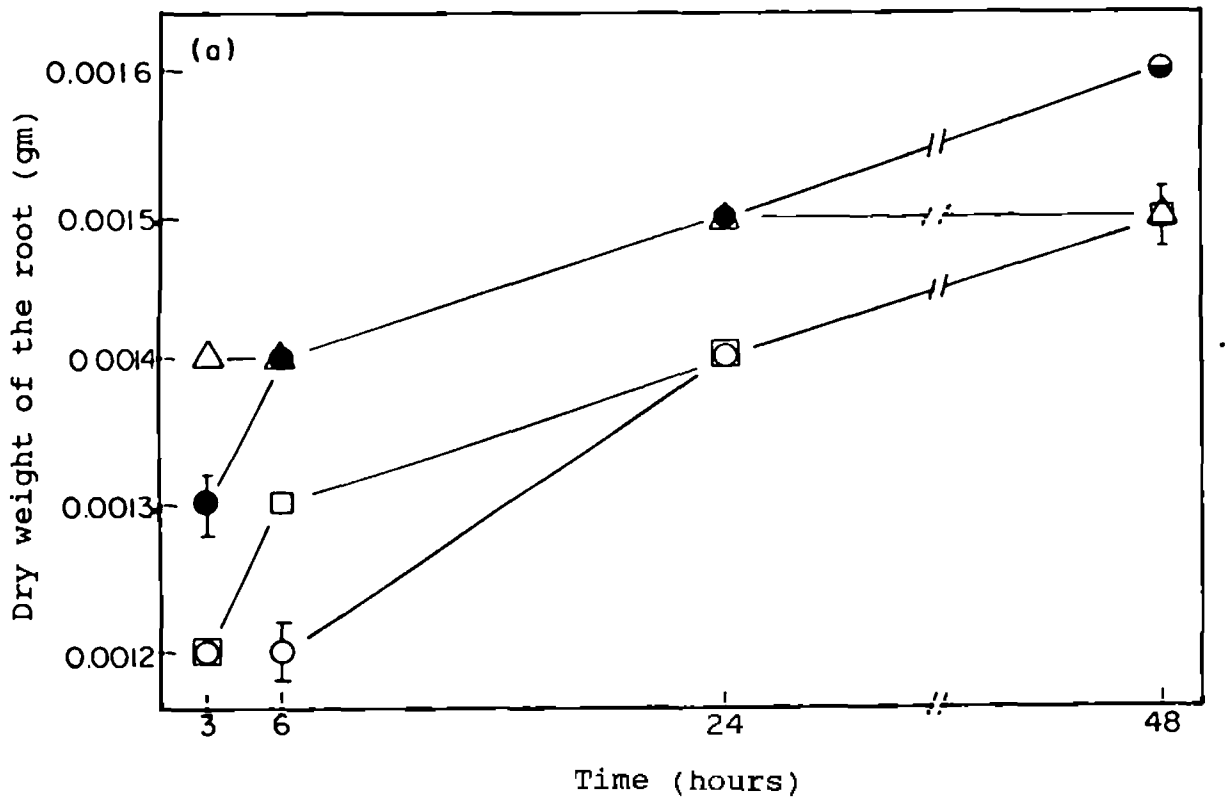

Fig. 37a. The effect of ABA on the root growth of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise was Fig. 11.

The shoot growth of intact rice seedlings was inhibited by 6.1 to 10.4% by 10^{-7} M at 24 to 48 hours of treatment (Fig. 37b). 10^{-6} M ABA did not show any significant effect on shoot growth (Fig. 37b). At the concentration of 10^{-5} M, ABA inhibited shoot growth by 7.6 to 11.6% from 6 to 48 hours of treatment in intact seedlings (Fig. 37b).

5.3.6. The effect of kinetin in the growth of intact rice seedlings

The root growth of intact rice seedlings was increased by 5.5 to 10.5% by 10^{-7} M kinetin at 24 to 48 hours of treatment but had no effect at 3 to 6 hours of treatment (Fig. 38a). 10^{-6} M kinetin did not show any significant effect on root growth (Fig. 38a). At the concentration of 10^{-5} M, kinetin increased root growth by 10.5% at 48 hours of treatment in intact seedlings (Fig. 38a).

The shoot growth of intact rice seedlings was increased by 13.1% by 10^{-7} M kinetin at 3 hours of treatment and the stimulatory effect was maintained up to 24 hours of treatment (Fig. 38b). 10^{-6} M kinetin caused an increase in shoot growth by 18.0 and 10.2% at 3 and 24 hours of treatment respectively (Fig. 38b). At the concentration of 10^{-5} M, kinetin also caused an increase in shoot growth by 27.8 to 12.5% at 3 to 48 hours of treatment in intact seedlings (Fig. 38b).

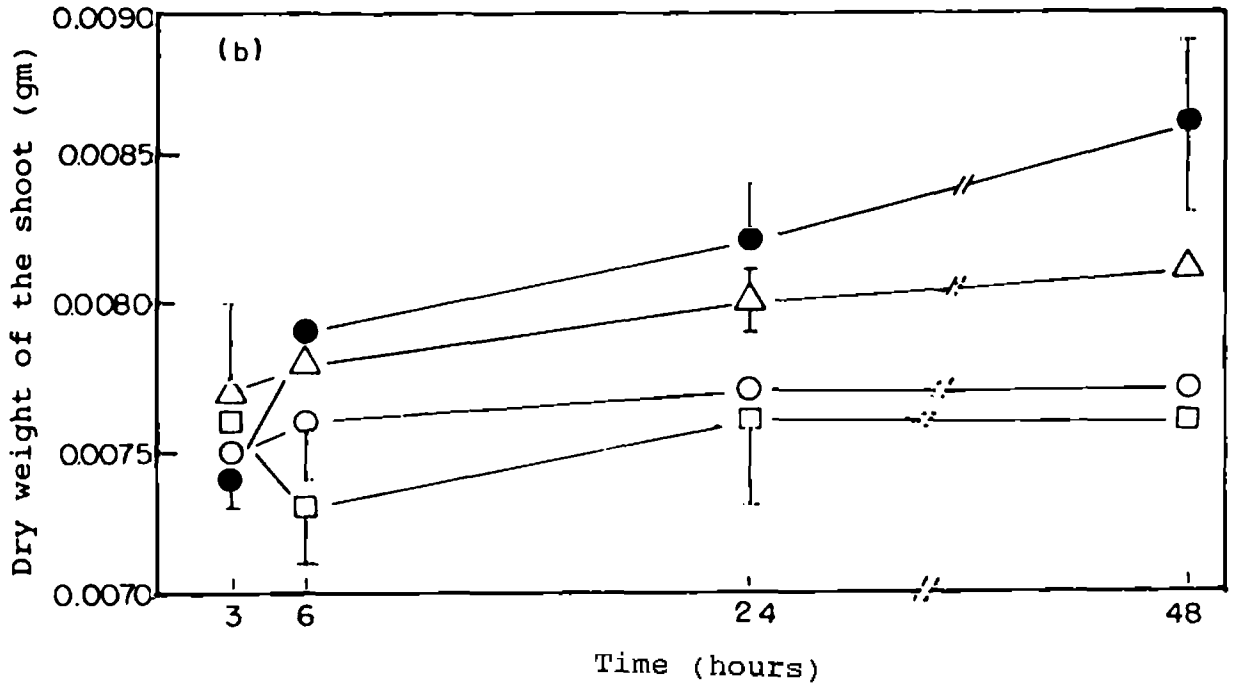

Fig. 37b. The effect of ABA on the shoot growth of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise was Fig. 11.

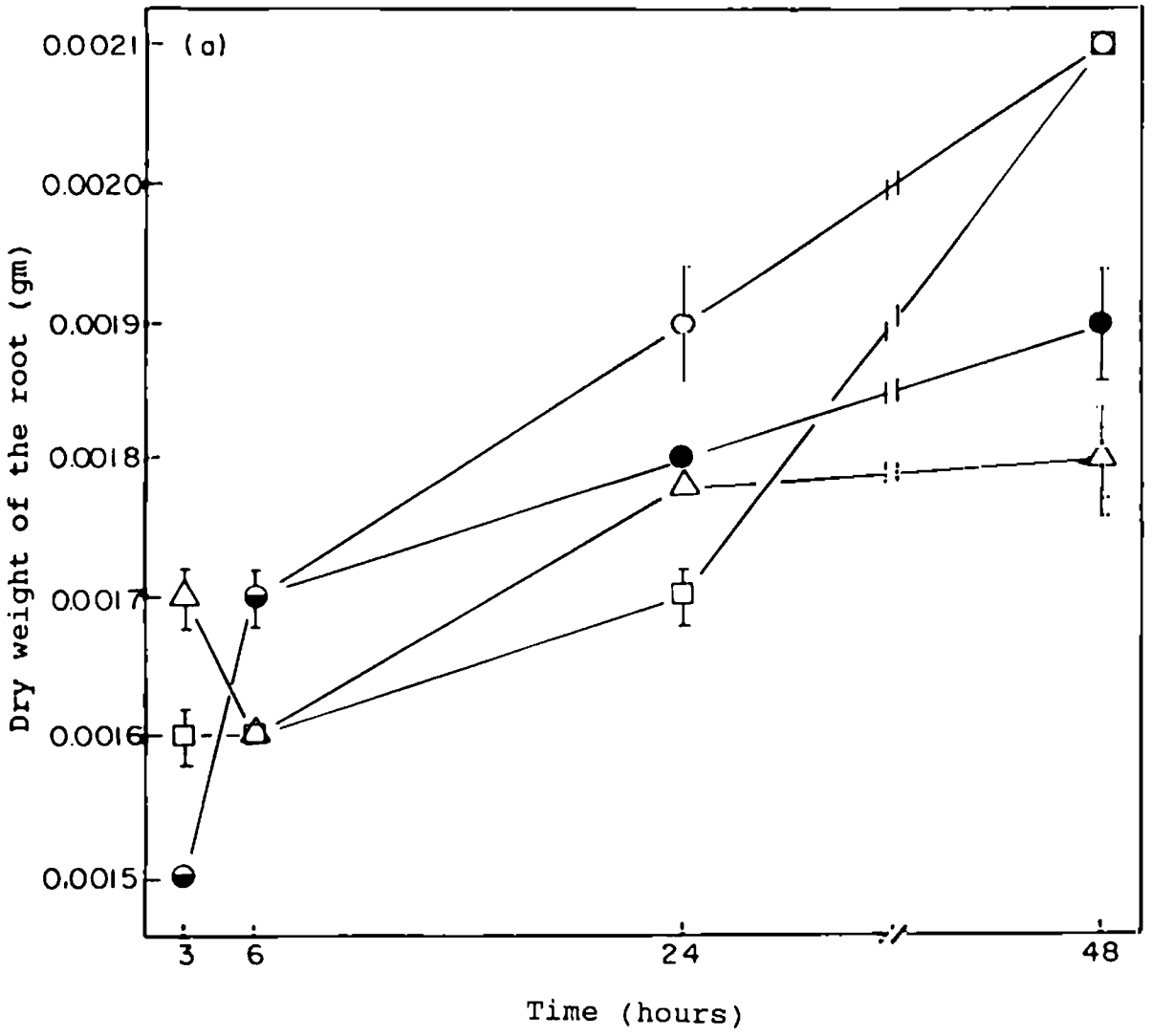

Fig. 38a. The effect of kinetin on the root growth of intact rice seedlings placed in half strength Hoagland solution with or without kinetin. Otherwise was Fig. 16.

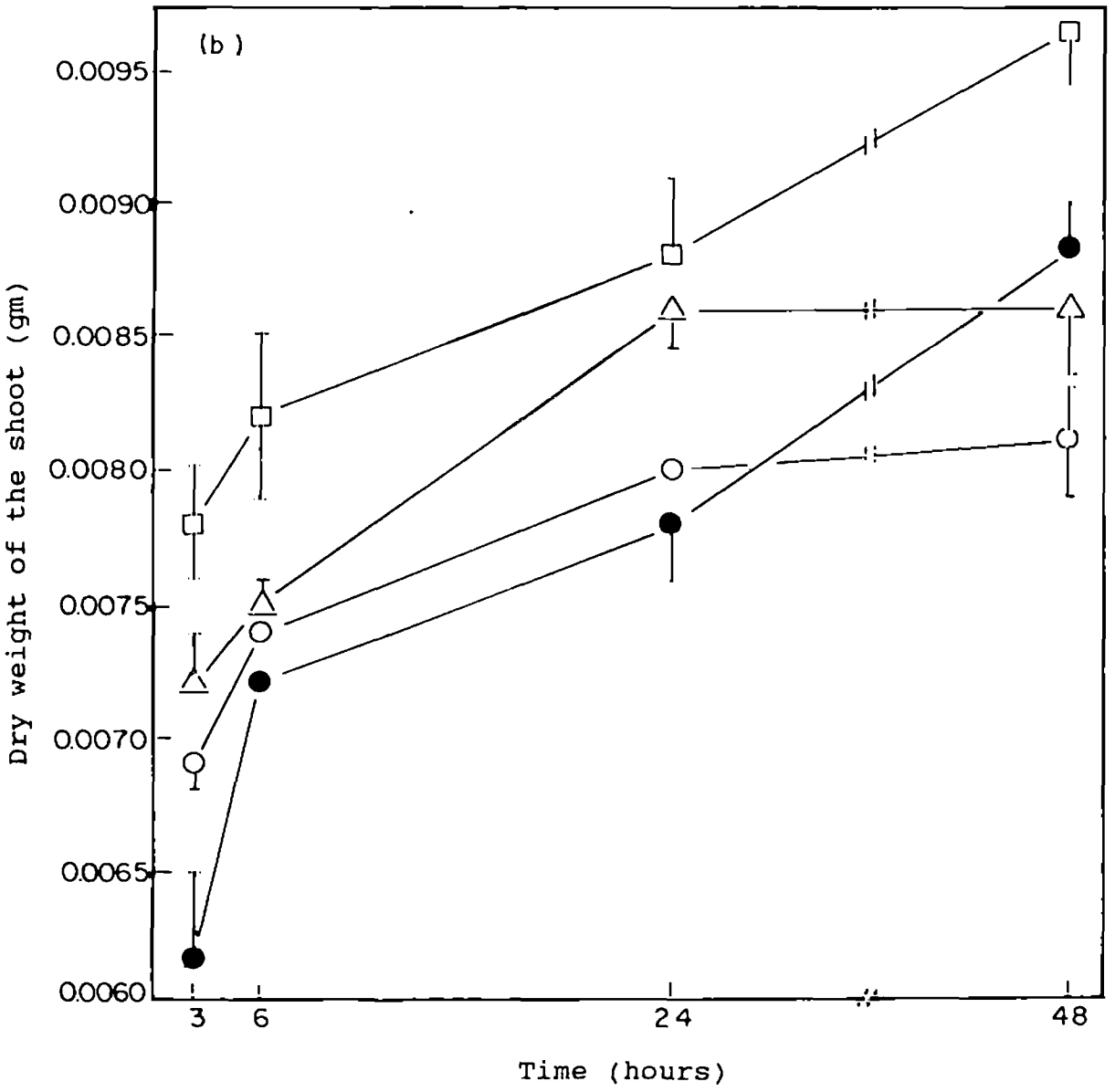

Fig. 38b. The effect of kinetin on the shoot growth of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise was Fig. 16.

5.4. Discussion

ABA increased Cl^- accumulation in the root and the shoot of intact rice seedlings (Fig. 31a and 31b). Similarly, Karmoker and Van Steveninck (1979a) reported that ABA increased Cl^- accumulation in the root of intact bean seedlings. On the other hand, ABA-induced 49% inhibition of ^{36}Cl transport into the shoot and 19% increase of ^{36}Cl accumulation in the root of intact barley seedlings were reported (Cram and Pitman 1972).

ABA increased NO_3^- accumulation in the root but decreased in the shoot of intact rice seedlings (Fig. 32a and 32b). This shows that ABA may be inhibitory to NO_3^- accumulation in the shoot but stimulatory to NO_3^- accumulation in the root. The stimulatory effect of ABA on NO_3^- accumulation was supported by Dekock *et al.* (1978) who found that higher concentration of ABA (1-100 ppm) increased NO_3^- content in *Lemna gibba*. Ullrich and Kunz (1985) showed a relationship between the effect of ABA on nitrate uptake, respiration and photosynthesis. They found that in unicellular green algae *Chlorella fusa* and *Ankistrodesmus* (*Monorhaphidium*) *braunii*, nitrate uptake was stimulated by 20 μM ABA in the light and in the dark and NO_3^- uptake was increased up to 200% by ABA (500 μM). The intracellular level of glucose was also increased in the presence of ABA. According to them increased starch degradation apparently may be involved in ABA-induced stimulation of respiration and nitrate metabolism rather than direct interference with the plasmalemma.

ABA inhibited phosphate accumulation in the root and the shoot of intact rice seedlings (Fig. 33a and 33b). Similarly, Dekock *et al.* (1978) found an inhibition of phosphate content by the influence of ABA at a higher concentration (1-100 ppm) in *Lemna gibba*. Treatment of the tuber of potato with ABA (10^{-4} M) did not change the ^{32}P distribution within the plants while foliat spray with ABA greatly increased the transport of ^{32}P into the tuber (Poder *et al.* 1988).

Hourmant and Penot (1978b) reported that ABA caused a partial inhibition of phosphate uptake in aged potato tuber disc but induced a stimulation of respiration. This indicates that hormone-induced inhibition of phosphate uptake was related to changes in respiration (Hourmant and Penot 1978b).

ABA stimulated net influx (Ψ_{OC}) of Cl^- after an initial decrease (Table 12). Similarly, Karmoker and Van Steveninck (1979a) reported that the net influx of Cl^- either increased or remained constant by ABA in intact seedlings. At the same time, fluxes of Cl^- into root vacuole were increased. The stimulation of the net influx of Cl^- indicates that ABA may affect the Cl^- pump situated at the root. ABA (10^{-6} and 10^{-5} M)) also stimulated the long distance transport (Ψ_{CX}) of Cl^- after an initial decrease (Table 12). A contradictory result was found in intact bean seedlings (Karmoker and Van Steveninck 1979a).

ABA inhibited both net influx (Ψ_{oc}) and long distance transport (Ψ_{cx}) of NO_3^- in intact rice seedlings (Table 13). Inhibition of net influx indicates that ABA directly affect the influx of NO_3^- into the root cytoplasm. The inhibition of long distance transport of NO_3^- may be due to the decrease in net influx.

ABA inhibited net influx (Ψ_{oc}) and long distance transport (Ψ_{cx}) of phosphate in intact rice seedlings (Table 13). It is apparent from this result that ABA decreased ATPase pump involved in phosphate influx. A decrease in net influx of phosphate lead to a decrease in long distance transport of this ion.

Kinetin (10^{-7} and 10^{-6} M) inhibited Cl^- accumulation in the root of intact rice seedlings (Fig.34a). The inhibitory effect of kinetin on Cl^- uptake and transport was also reported in intact bean seedlings (Karmoker 1981). On the other hand, kinetin (10^{-6} and 10^{-5} M) increased the accumulation of Cl^- in the shoot of intact rice seedlings (Fig. 34b). The stimulatory or inhibitory effect of kinetin on Cl^- accumulation may be due to the effect of kinetin on Cl^- pump.

Kinetin (10^{-7} and 10^{-6} M) inhibited NO_3^- accumulation in the root of intact rice seedlings (Fig. 35a). But NO_3^- accumulation on the shoot of intact rice seedlings was stimulated by kinetin (Fig. 35b). Reports regarding the effect of kinetin on NO_3^- accumulation is very rare.

Kinetin stimulated phosphate accumulation in the root and the shoot of intact rice seedlings (Fig. 36a and 36b). On the contrary, kinetin was found to inhibit phosphate transport in the cellular mass of *Chlorella pyrenoidosa* cultifvars (Torre and Liliana 1987).

Kinetin inhibited net influx (Ψ_{oc}) and long distance transport (Ψ_{cx}) of Cl^- in intact rice seedlings (Table 15). Similarly Karmoker and Razia (1993) reported that kinetin inhibited net influx and long distance transport of Cl^- in intact rice seedlings.

Kinetin increased net influx (Ψ_{oc}) and long distance transport (Ψ_{cx}) of No_3^- in intact rice seedlings (Table 16). Increase in net influx of NO_3^- indicates that kinetin stimulated the pumping mechanism of this ion into the root cytoplasm. The increase in long distance transport of NO_3^- might result from the increase in net influx.

Kinetin increased both net influx (Ψ_{oc}) and long distance transport (Ψ_{cx}) of phosphate in intact rice seedlings (Table 17). It is apparent from the stimulation of net influx of phosphate that kinetin increase the pumping of ATP through the plasmalemma. The increase in long distance transport of phosphate may result from the increase in net influx.

A relation between phytohormone-induced growth and ion transport are also reported in this chapter. ABA inhibited the root and

the shoot growth of intact rice seedlings (Fig. 37a and 37b). Similarly, ABA inhibited the uptake and transport of K^+ and Na^+ in the root and shoot of intact rice seedlings (Fig. 21a, 21b, 22a and 22b). It appears that ABA-induced growth of root and shoot is related with ABA-induced K^+ and Na^+ transport in intact seedlings. On the other hand, ABA decreased Fe^{2+} and phosphate in the root and shoot of intact rice seedlings (Fig. 25a, 25b, 33a and 33b). But ABA-induced inhibition of Fe^{2+} and phosphate accumulation was large as compared to ABA-induced decrease in growth. This indicates that in this case, the inhibition of ion transport is not related with phytohormone-induced growth, although a relation between growth and ion transport was suggested by Steward and Sutcliffe (1959). ABA increased the accumulation of Ca^{2+} and Cl^- in the root and the shoot of intact rice seedlings (Fig. 23 a, 23b, 24a, 24b, 31a and 31b). In this case, ABA-induced inhibition of growth showed negative relation with these ions. On the other hand, ABA increased Mg^{2+} and NO_3^- accumulation in the root but decreased in the shoot (Fig. 24a, 24b, 32a and 32b). So, there is no relation between ABA-induced growth Mg^{2+} and NO_3^- accumulation.

Kinetin increased the growth of root and shoot in intact rice seedlings (Fig. 38a and 38b). On the other hand, kinetin decreased K^+ and Cl^- accumulation in the root but increased in the shoot (Fig. 26a, 26b, 34a and 34b). Na^+ accumulation decreased in the shoot but increased in the root by the influence of kinetin in intact rice seedlings. It can be concluded from

these results that there is no relation between kinetin-induced growth and those in ion transport in intact seedlings. Kinetin decreased the accumulation of Ca^{2+} in the shoot of intact rice seedlings (fig. 28b). This indicates that kinetin-induced growth showed negative relation with Ca^{2+}. But the effect of kinetin on ion transport is larger than that on the growth. This indicates that kinetin may affect the ion pumps.

CHAPTER 6

Mechanistic aspects of hormonal regulation of ion transport

Section 6a

The effect of abscisic acid on sugar level and its correlation with transport of ions in intact rice seedings

6a.1. Introduction

Phytohormone plays an important role in metabolites transport (Peel 1974, Phillips 1975, Patrick 1976). As for example, IAA (30 ppm) caused a maximum increase in total proteins and GA_3 (100 ppm) caused a stimulation of carbohydrate and phenol level in *Trigonella foenum graecum* L. (Jain and Agrawal 1987). Kadioglu and co-workers (1991) reported that the carbohydrate content of *Chlamydomonas reinhardii* and *Anacystis nidulans* was substantially increased by 50 μM IAA, benzyladenine and gibberellic acid. IAA-stimulated accumulation and transport of metabolites were also reported in *Phaseolus vulgaris* (Altman and Wareing 1975, Patrick and Wareing 1973). Datta and Katsumi (1989) reported that GA caused a decrease in sucrose content but had no significant effect on the levels of other sugars in the leaf sheath of dwarf maize. GA stimulated the net influx of soluble sugars, starch and cell wall polysaccharide to the epicotyl and the net outflow from cotyledons in derooted *Pisum sativum* (Miyamoto and KamisakaI990). Miyamoto and co-workers

(1992) reported that GA stimulated the sugar exudation and invertase activity in epicotyls in growing subhooks of etiolated *Pisum sativum* seedlings. They suggested that GA-induced stimulation of sugar accumulation in the growing subhook was found due to the stimulation of loading (in the cotyledons) and unloading (in the subhook) of sucrose in the phloem. ABA inhibited the sugar content in *Coleus blumici* (Kuhl and Unger 1974) while it stimulated sugar and starch levels in *Lemna minor* (Mclaren and Smith 1976). Karmoker and Van Steveninck (1979a) showed that ABA promptly increased the accumulation of reducing and total sugar in the root of intact bean seedlings. They proposed that a relationship may exist between sugar level and ion transport. A correlation between sugar level and ion transport was also found in barley roots (Pitman *et al.* 1971).

6a.2. Materials and Methods

6a.2.1. Culture of plants

Plants were grown following the method described in 2.4.

6a.2.2. Methods of ion transport experiment with intact seedlings

Ion transport experiment was performed following the technique described in 2.6.

Stock solution of ABA was prepared according to 2.3.4. ABA was used at concentration of 10^{-7}, 10^{-6} and $1o^{-5}$ M.

6a.2.3. Collection of sample

Samples were collected according to the method described in 2.7.

6a.2.4. Method of the extraction of sugar

Sugar was extracted according to the method described in 2.9.1.

6a.2.5. Measurement of sugar in intact plant

Reducing sugar was measured according to the method described in 2.9.2.

Total sugar was measured according to the method described in 2.9.3.

6a.3. Results and Discussion

In the root of intact rice seedlings, 10^{-7} M ABA increased reducing sugar content by 5.5, 18.4 and 13.6% at 6, 24 and 48 hours of treatment respectively after an initial decrease of 10.0% at 3 hours of treatment (Fig. 39a). Similarly, 10^{-6} M ABA also increased reducing sugar content in roots by 13.8% at 6 hours of treatment and the stimulatory effect was maintained up to 48 hours of treatment (Fig. 39a). ABA, at the concentration of 10^{-5} M, caused an increase in reducing sugar content by 15.7% at 24 hours of treatment (Fig. 39a). These results are supported by Karmoker and Van Steveninck (1979b) who found that ABA caused a 3-fold increase in reducing sugar content in the root of intact rice seedlings.

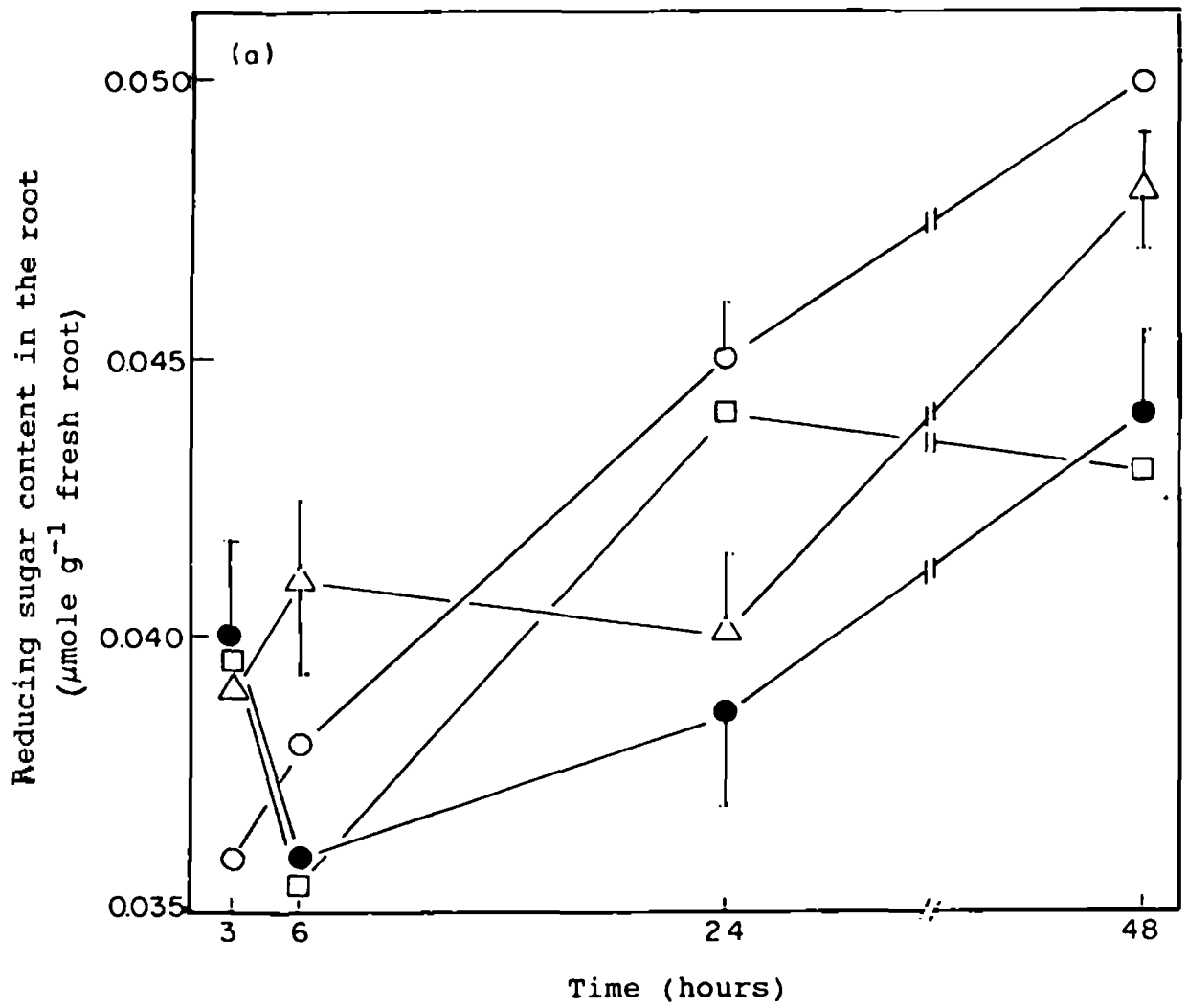

Fig. 39a. The effect of different concentrations of ABA on reducing sugar content in the root of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

In the shoot of intact rice seedlings, 10^{-7} M ABA inhibited reducing sugar content by 7.1, 37.5 and 32.0% at 6, 24 and 48 hours of treatment respectively after an initial increase by 11.7% at 3 hours of treatment (Fig. 39b). ABA, at 10^{-6} M, stimulated reducing sugar content by 42.8% at 6 hours of treatment. However, the reducing sugar content in the shoot declined by 12.5 to 8.3% at 24 to 48 hours of treatment (Fig. 39b). On the other hand, 10^{-5} M ABA increased reducing sugar content by 71.4% at 6 hours of treatment. The reducing sugar level in treated plant was nullified with the control at 24 to 48 hours of treatment (Fig. 39b). Similarly, ABA was found to increase the level of reducing sugar content in the stem of intact bean seedlings (Karmoker and Van Steveninck 1979b).

In the root of intact rice seedlings, 10^{-7} M ABA increased total sugar content by 8.3 and 7.1% at 24 and 48 hours of treatment respectively after an initial inhibition at 3 to 6 hours of treatment (Fig. 40a). ABA, at 10^{-6} M, did not show any significant effect on total sugar content in the root (Fig. 40a). At the concentration of 10^{-5} M, ABA caused a stimulation of total sugar content by 27.8 to 10.0% at 3 to 48 hours of treatment (Fig. 40a). The increase of sugar level may have been resulted from an increased hydrolysis of starch reserved in the root initiated by ABA.

In the shoot of intact rice seedlings, 10^{-7} M ABA did not show any significant effect on total sugar content at 6 to 48 hours of

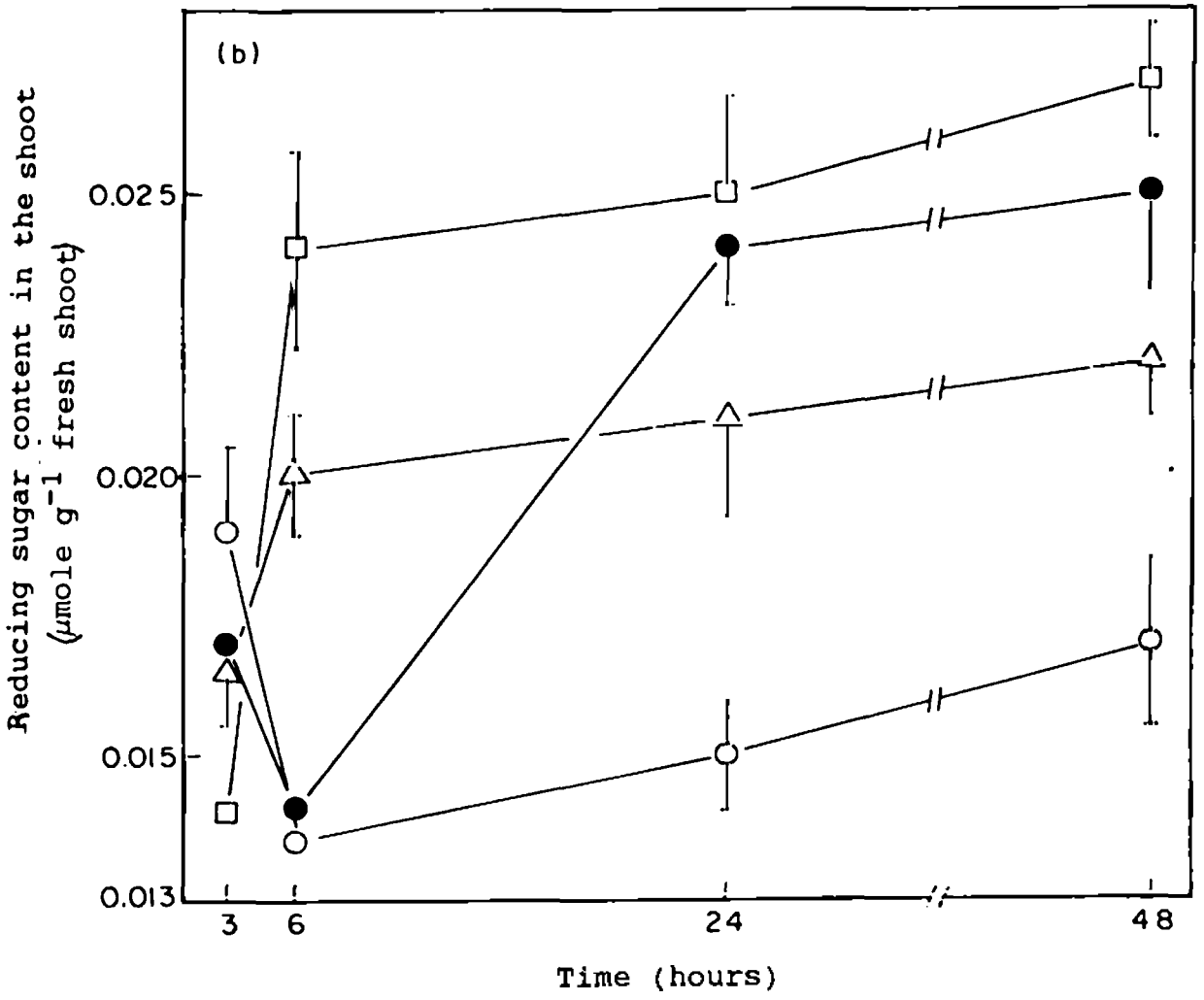

Fig. 39b. The effect of different concentrations of ABA on reducing sugar content in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

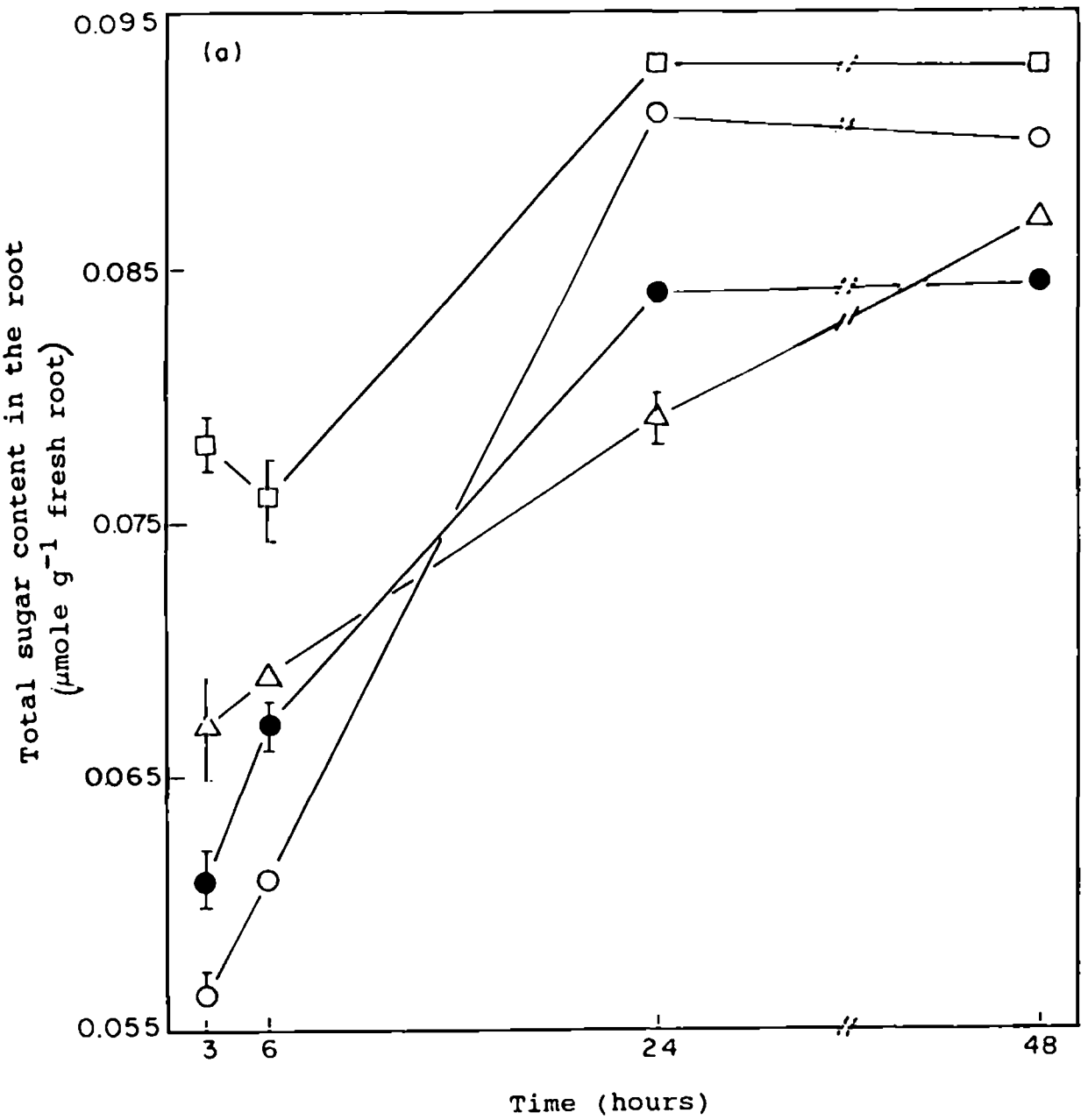

Fig. 40a. The effect of different concentrations of ABA on total sugar content in the root of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

treatment (Fig. 40b). At the concentration of 10^{-6} and 10^{-5} M, ABA increased total sugar content by 28.0 to 15.1% and 12.2 to 16.6% respectively at 24 to 48 hours of treatment in the shoot (Fig. 40b). It was suggested that ABA increased sugar level in plants due to the inhibition of the formation of starch from assimilates which was produced in the leaves (Mittelheuser and Van Steveninck 1972).

Karmoker and Van Steveninck (1979b) reported that ABA increased reducing sugar content and total sugar content in the roots of intact bean seedlings and the level of reducing sugar was also increased in the shoot but the level of total sugar content remained unaffected by ABA. Ullrich and Kunz (1985) showed that the intracellular level of glucose stimulated the presence of ABA in *Chlorella fusa* and *Ankistrodesmus* (*monorhaphidium*) *braunii*.

It was found that ABA decreased the accumulation of K^+ and Na^+ in the root and shoot of intact rice seedlings (Chapter 4). The net influx and long distance transport of those ions also decreased by ABA in intact rice seedlings (Chapter 4). It appears that ABA-induced stimulation of sugar level (both reducing and total sugar) in intact rice seedlings (Fig. 39a, 39b, 40a and 40b) is negatively correlated with ABA-induced inhibition of K^+ and Na^+ accumulation in the root and shoot (Fig. 21a, 21b, 22a and 22b).

Hutchings (1978a) reported that Rb^+ (K^+) influx decreased by 32% in the presence of 10 mM sucrose. It was suggested that an interaction between ABA-induced increase in sugar level and the action of ABA on overall ion transport might have occurred in the

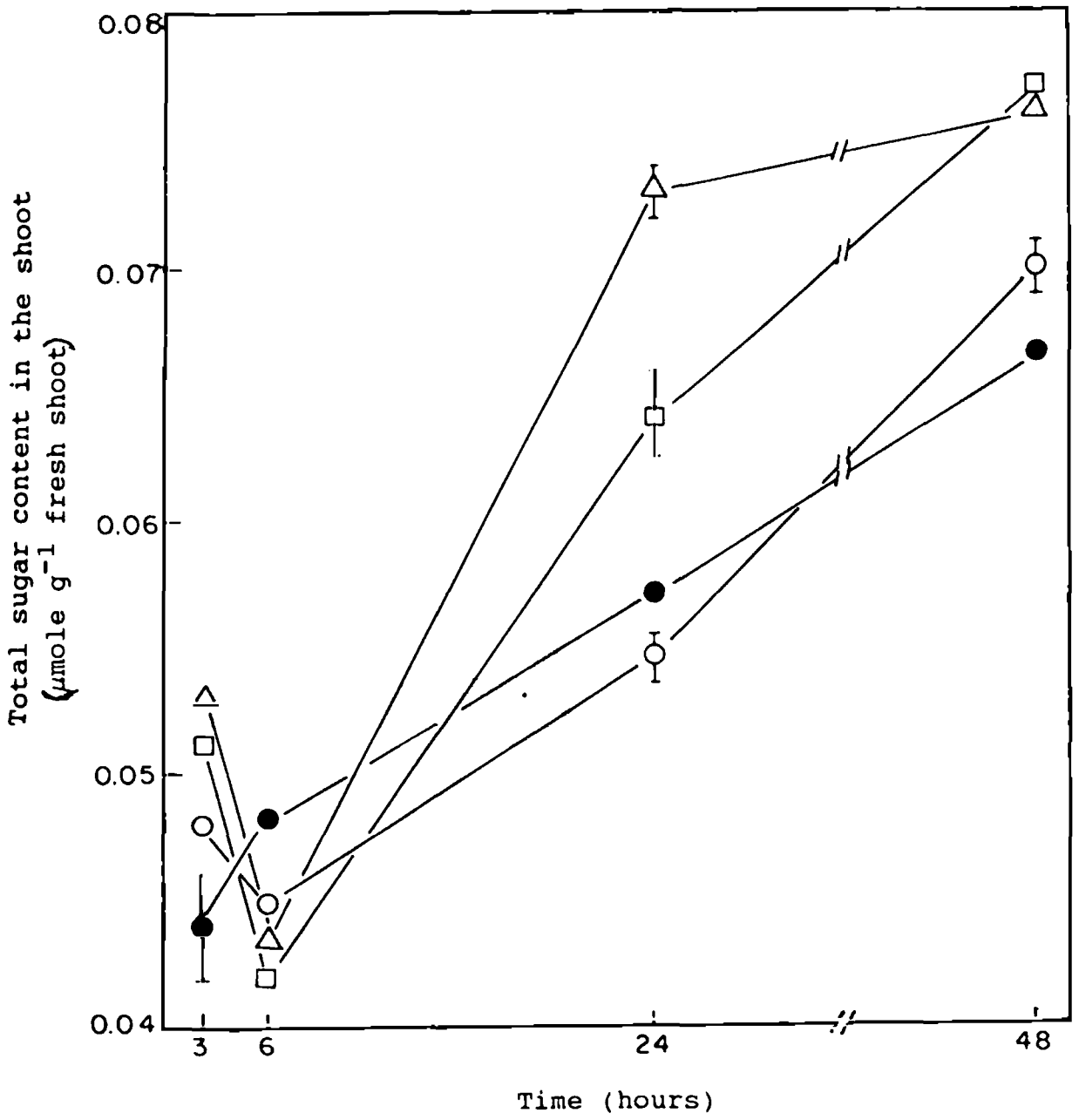

Fig. 40b. The effect of different concentrations of ABA on total sugar content in the shoot of intact rice seedlings placed in half strength Hoagland solution with or without ABA. Otherwise as Fig. 11.

root of intact seedlings (Karmoker 1929b). A relationship between sugar level and ion transport was also reported in barley root (Pitman *et al.* 1971).

However, a stimulation of downward transport of sugar from the shoot to the root systems (Karmoker and Van Steveninck 1979b) may be associated with an stimulation of ion transport in phloem because co-transport of sugar and inorganic ions have been reported (Mengel and Haeder 1977, Hutchings 1978a, 1978b).

Thus, it can be made possible in this way that the divergent effect of ABA on ion transport in the root and shoot may be related to an additional effect of ABA on sugar level and sugar transport.

Section 6b

The effect of abscisic acid on H^+ efflux from roots and its correlation with transport of ions in intact rice seedings

6b.1. Introduction

Fusicoccin (Fc) stimulated H^+ efflux, K^+ uptake and growth in a number of tissues. As a result of that, the hyperpolarisation of cell potential difference (PD) occurred by Fc (Marre *et al.* 1974). Similarly, H^+ efflux was found to rapidly initiated by Fc with a concomitant stimulation of K^+ influx and hyperpolarisation of cell PD in barley roots (Pitman *et al.* 1975). So, there might be a electrogenic coupling between Fc-stimulated H^+ efflux and cation uptake. Lado *et al.* (1976) reported that Fc showed a marked increase in H^+ extrusion and K^+ uptake but had little or no effect on Na^+ or other monovalent cations. A selectivity between K^+ and Na^+ was also reported by Rains and Epstein (1967). Pitman *et al.* (1968) showed a increase in selectivity of K^+ relative to Na^+ during the accumulation of K^+ and Na^+. IAA (10^{-5} M) also stimulated H^+ extrusion from sunflower hypocotyle segments (Hager *et al.* 1971). Evans *et al.* (1980) reported that IAA and L-naphthalene acetic acid increased H^+ extrusion from corn roots. On the other hand, auxin-induced H^+ extrusion was completely inhibited at higher concentration (5×10^{-5} M) of ABA but partially inhibited at lower concentration ($5 \times I0^{-7}$ M) of ABA (Rayle 1973). Karmoker (1981) reported that ABA inhibited both H^+ extrusion and K^+ transport in intact bean root systems.

Schubert and Matzke (1985) showed that IAA promoted but ABA inhibited the net H^+ release from isolated protoplast of rape leaves. It was found that ABA inhibited H^+ extrusion and K^+ uptake with a simultaneous depolarisation of membrane electric potential (MP) in wheat coleoptile segments (Stolarek and Zientara 1991).

6b.2. Materials and Methods

6b.2.1. Culture of plants

Plants were grown following the method described in 2.4.

6b.2.2. Methods of ion transport experiment with intact plants

Ion transport experiment was performed following the technique described in 2.6.

Stock solution of ABA was prepared according to 2.3.4.

Plants were then allowed to grow for 24 hours. The initial pH of the half Hoagland solution was recorded.

6b.2.3. Measurement of H^+ extrusion

The pH of the experimental solution became acidic at the end of the experiment. Net H^+ extrusion was measured by titration of the experimental solution with 5 mM KoH. Before titration, roots were separated from the shoot and roots were left in the

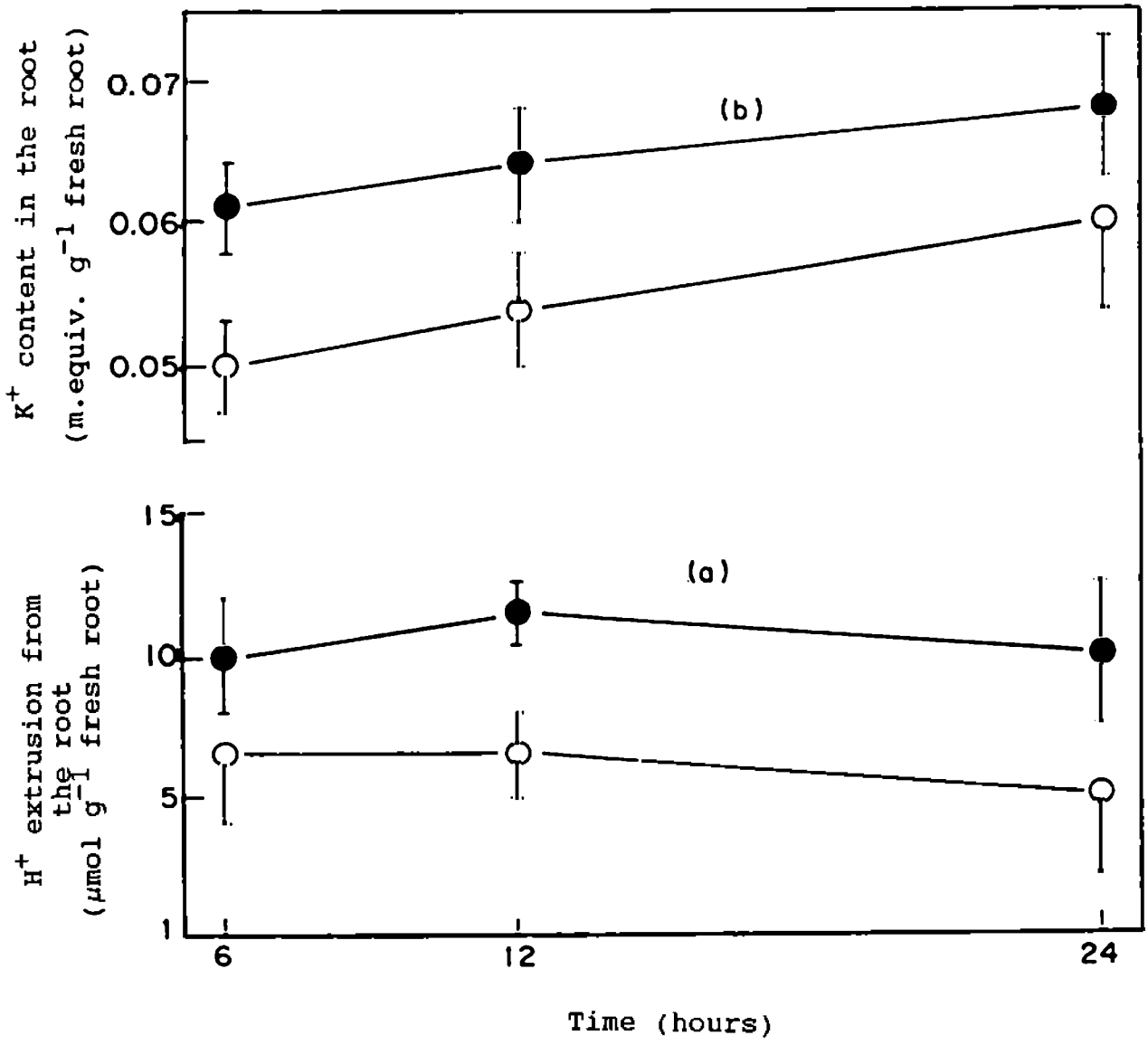

Fig. 41. The effect of 10^{-6} M ABA on (a) H^+ extrusion and (b) K^+ accumulation in the root systems of intact rice seedlings placed in half strength Hoagland solution with or without ABA. (O) represents control; (O) H^+ extruction.

solution. The experimental solution along with roots was titrated to the initial pH (5.5) of the growth medium.

6b.3. Results and Discussion

ABA (10^{-6} M) decreased H^+ extrusion from root at 6, 12 and 24 hours of treatment with a concomitant decrease in K^+ accumulation (Fig. 41). This result was supported by the work of Karmoker (1981) who found that ABA inhibited H^+ extrusion and K^+ uptake in intact bean seedlings. Recently, Stolareck and Zientara (1991) also found similar result in wheat coleoptile segments. It is suggested that the present result (Fig. 41) supportd the cation exchange theory. For example, when the H^+ extrusion is decreased, there is less exchange of K^+ for H^+, thereby decreasing the uptake of K^+.

CHAPTER 7

Conclusion

Results from the present investigation (described in previous chapters) regarding the effect of ABA and kinetin on ion transport support the view that phytohormones are involved in the regulation of ionic balance in plants (Karmoker 1984).

ABA caused a decrease in the accumulation of K^+ and Na^+ in the excised root systems of rice seedlings (Chapter 3). ABA also decreased K^+ and Na^+ accumulation in intact rice seedlings (Chapter 4). The effect of ABA on K^+ and Na^+ on excised root may be reconciled with that in intact plant. On the contrary, it was found that following ABA treatment K^+ transport was increased in excised root systems (Karmoker and Van Steveninck 1978) but decreased in intact plant in bean seedlings (Karmoker and Van Steveninck 1979a). Therefore, it is proposed that ion pumps in monocotyledonous root systems (eg. rice) differs from that of dicotyledonous root systems (eg. bean) with respect to their response to abscisic acid.

The inhibitory effect of ABA on ion transport may be influenced by the effect of ABA on different physiological process. As for example, ABA-induced decrease in transpiration rate of intact seedlings (Little and Eidt 1968, Mizrahi *et al.* 1970) may lead to decrease in transfer of ion from the xylem vessels. As a result an ionic concentration may build up in the xylem sap.

ABA may induce a stimulation in recirculation of K^+ (Ben Zioni *et al.* 1971, Armstrong and Kirby 1979) which lead to a decrease of K^+ accumulation in the shoot. ABA-induced stimulation of endogenous ABA level may lead to a decrease in ion transport in intact plants (Karmoker and Van Steveninck 1979a). ABA-induced closure of stomata (Mittleheuser and Van Steveninck 1969, 1971, Cummins *et al.* 1971, Kriedemann *et al.* 1972) may result in a positive pressure counteracting root pressure. ABA-induced inhibition of ion transport may be due to ABA-induced inhibition of ATPase activity in plants (Maslowski *et al.* 1974).

ABA inhibited net influx and long distance transport of K^+, Na^+, NO_3^- and phosphate in intact rice seedlings (Table 2, 3, 13 and 14). The uptake and long distance transport of ions may be controlled through a negative feedback system in ABA-treated seedlings (Karmoker 1981).

ABA showed a inhibitory effect on Ca^{2+} and Mg^{2+} accumulation in excised root systems but increased the accumulation of those ions in intact plant (Fig. 13, 14, 23a and 24b). So, ABA exerts differential effects on divalent cation.

ABA increased reducing and total sugar content in intact rice seedlings (Chapter 6, Section 6a). An interaction between the effect of ABA on sugar level and its effect on ion transport may be involved in the inhibition of ion transport (Pitman *et al.* 1971, Karmoker and Van Steveninck 1979b).

ABA inhibited H^+ efflux with a concomitant inhibition of K^+ transport in intact rice seedlings (Chapter 6, Section 6b). ABA-induced inhibition in H^+ efflux may result in inhibition of K^+ transport due to the effect of ABA on cation exchange.

Kinetin stimulated the accumulation of Mg^{2+}, Fe^{2+} and phosphate in intact rice seedlings (Fig. 29a, 29b, 30a, 30b, 36a and 36b). Kinetin-induced stimulation of Mg^{2+}, Fe^{2+} and phosphate transport may be due to a number of reasons. As for example, kinetin-induced hyperpolarization (Abutalybov *et al.* 1980) increases the driving force for cation transport along the electrochemical gradient (Marre 1979) which lead to stimulation of ion transport. Protein might act as carrier of ion transport across the plasmamembrane and in ion transport from the symplasm into the xylem (Schaefer *et al.* 1975). The stimulatory effect of kinetin on ion transport can be explained in the light of kinetin-induced stimulation of protein synthesis (Mothes *et al.* 1961, Gunning and Barkley 1963) in terms of a carrier concept.

Kinetin inhibited net influx and long distance transport of Na^+, Ca^{2+} and Cl^- (Table 8, 9 and 15). A continuous supply of kinetin may cause an imbalance in endogenous hormone level and also lead to supra- or sub-optimal concentration of endogenous kinetin which in turn could have inhibitory effects on ion transport in plant (Karmoker 1982).

Kinetin increased net influx and long distance transport of NO_3^- and phosphate (Table 16 and 17). The increase in NO_3^- and phosphate level may be related to nitrogen and phosphorus-

dependent physiological and biochemical process like N_2 metabolism and lipid metabolism. Besides, a correlation between phytohormone-directed transport of ions and phytohormone-induced changes in respiration was established (Palmer 1966, Hourmant and Penot 1978b, Karmoker and Van Steveninck 1979a). Palmer (1966) reported that kinetin inhibits phosphate uptake which was associated with the inhibition of respiration and invertase activity. A partial inhibition in increased rate of respiration and phosphate uptake was found in aged potato tuber discs in the presence of the analogues of kinetin like BAP (benzylaminopurine), MAP (methylaminopurine) and FAP (furfurylaminopurine).

Further studies on the effect of ABA and kinetin on membrane-bound ATPase and other enzymes related to ion transport protein/lipid composition may help in understanding the mechanism of their actions. In this respect, it may be relevant to study the ultrastructural changes that may occur due to prolonged exposure to external hormones.

Finally, the fundamental information obtained through the present investigation on phytohormone directed ion transport may be useful in understanding the mechanism of ionic relation under stress conditions where plants are subjected to a major change in hormonal balance.

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