

Effects of Al-Surplus and Ca-Deficiency on Content and Rhythm of ATP in Plant Leaves

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植物葉의 ATP含量과 그 週期에 미치는 Al過剩 및 Ca缺乏의 影響

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ABSTRACT

Kidneybean(*Phaseolus vulgaris* L.) and buckwheat(*Fagopyrum esculentum* Mönch) seedlings cultured with Hoagland solution to the height of 7 to 10 cm in the earthen pot containing sand were used for experimental plants. One group of the plants was irrigated with Hoagland solution composed of various Al concentrations of 0 to 1,000 ppm containing 50 ppm Ca, and the other group was irrigated with Hoagland solution composed of various Ca concentrations of 0 to 1,000 ppm containing 100 ppm Al for a month during June and July.

By Al-surplus over 100 ppm, the margins of buckwheat leaves were curled down and turned into yellow-brown necrosis similar to Ca-deficiency, and the old kidneybean leaves showed marginal and veinal chlorosis in addition to the early shedding of leaves. With Al-surplus of 100 ppm the content of chlorophyll a and b in both plants was decreased by 30~40%. The ratio 3/1 of chlorophyll a/b was not altered by Al-surplus and Ca-deficiency at an early stage, but it was affected markedly at a final stage of growth. Leaf respiration with 100 ppm Al containing 50 ppm Ca was slightly affected in buckwheat, but decreased by 20% in kidneybean. With Al-surplus of 100 ppm the ATP content was decreased by 32% in the kidneybean leaves and by 80% in buckwheat leaves, whereas with Ca-deficiency it was decreased by 72% in kidneybean and by 90% in buckwheat. The rhythm of ATP level showed self-reliance without being affected by light or temperature under the green house condition although by Al-surplus and Ca-deficiency the ATP level of the rhythm was lower than that of control.

INTRODUCTION

Al-toxicity has been reported generally to reduce the uptake and utilization of calcium (Edwards and Horton, 1977; Etherington, 1976; Foy *et al.*,

1969; Johnson and Jackson, 1961; Russel, 1973), and to induce a phosphate deficiency (Clarkson, 1967; Foy and Brown, 1963). Aluminum binds and precipitates phosphorus in the internal or on the external surface of plants, which means that less phosphorus is available for metabolic activities

within the cells (Clarkson, 1966; Edwards *et al.*, 1976; Wright, 1943; Wright and Donahue, 1953). Generally calcium as cofactor is required by some enzymes involved in the hydrolysis of ATP and phospholipids, whereas phosphorus is a component of sugar phosphates, nucleic acids, nucleotides and phospholipids in addition to the key role in ATP related reactions (Noggle and Fritz, 1976). The effect of aluminum on glucose phosphorylation are now known to impare the utilization of ATP by Al injury of acid phosphatase and ATPase in wheat seedlings (Takahashi, 1974). In the recent reports the heredity of the rhythm in bioluminescence was found in *Gonyaulax* (Kiessig *et al.*, 1979; Sweeny, 1979). However the effect of Al-surplus and Ca-deficiency on ATP content in plant leaves were not yet clearly defined.

The purpose of present study was to determine the effect of Al-surplus and Ca-deficiency with particular emphasis on ATP content and rhythm of ATP level in the prepared leaves.

MATERIALS AND METHODS

Plant Growth Kidneybean (*Phaseolus vulgaris* L.) and buckwheat (*Fagopyrum esculentum* Mönch) seedlings were germinated and grown with Hoagland solution to the height of 7 to 10 cm in 2 liter earthen pot containing sand previously washed with distilled water under the greenhouse condition for two weeks during June and July 1979. After the two weeks the seedlings were thinned out to 8 plants per pot. These plants were grown for a month with the following treatments; for one group, the concentrations of 0, 0.1, 1, 10, 100, and 1,000 ppm Al solutions were prepared from $AlCl_3$ with Hoagland solution containing 50 ppm Ca from $Ca(NO_3)_2$; and then 300 ml of each of the final solution was supplied to each of the Al-treatments on alternate day; for the other groups, the concentrations of 0, 0.1, 1, 10, 100 and 1,000 ppm Ca solutions were prepared from $Ca(NO_3)_2$ with Hoagland solution containing 50 ppm Al from $AlCl_3$, and then the final solutions were supplied to each of 'Ca treatments in the same way. The pH of culture solutions were adjusted to 6.5. The leaves of cultured

plants were collected to determine dry weight, chlorophyll content, respiration, ATP content, and the rhythm of ATP level.

Chlorophyll Content Chlorophyll a and b content were estimated by slight modification of the methods of Arnon (1949) with UV-190 Spectrophotometer.

Leaf Respiration The CO_2 amount evolved by leaf respiration was measured by the method previously mentioned (Sung, 1979).

ATP Content Leaf sample of 3 grams was boiled with 30 ml Tris buffer of pH 7.4 for three minutes to kill the cells rapidly and inactivate the ATPase contained in the cells themselves. The boiled leaf solution was replenished for evaporated moiety to 30 ml by adding some precooled Tris buffer solution and transferred to ice-jacketed homogenizer vessel. After homogenizing at 4,500 rpm, at 0°C, for 10 minutes, the homogenate was filtered through two layers of gauze. This filtrate was used to measure ATP content of the leaves. The ATP content of filtrate was determined by measuring the peak reading of a SAI Technology Co. 2000 ATP-Photometer which measures the fluorescence of 560~580 nm wavelength emitted by hydrolysis of ATP contained in 1 ml reaction mixture composed of 0.5 ml of the filtrate and 0.5 ml luciferin-luciferase, and referring the peak reading of the photometer to the standard curve of ATP.

Rhythm of ATP Level The leaves of both plants treated with Al and Ca concentrations were collected at intervals of three hours for a day on 25th, July 1979. To determine the rhythm of ATP level, the ATP content of the leaves were measured immediately after each of the leaf collections. The light intensity and temperature of the greenhouse during that day was recorded.

Because a proper conclusion for the rhythm of ATP level was difficult to be drawn with only two kinds of plants, we examined the leaves of four other kinds of plants grown normally for two months in the field. The latter four kinds of plants were soybean (*Glycine max* Merrill), peanut (*Arachis hypogaea* L.), sweet potato (*Ipomea batatas* Lamark), and perilla (*Perilla frutescens* Britton).

RESULTS AND DISCUSSION

Symptoms of Al-Toxicity Al-toxicity symptoms observed in the buckwheat leaves was curling down along the margins, ultimately developed into yellow-brown necrosis. However, Al-toxicity of 100 ppm in the old leaves of kidneybean caused typical marginal and veinal chlorosis. The above Al-toxicity symptoms were all similar to Ca-deficiency symptoms. The early shedding of leaves in the present study was also similar to P-deficiency and Ca-deficiency. Like P-deficiency, Al-toxicity symptoms of kidneybean leaves were observed to be chlorotic leaves and newly formed dark-green leaves as already reported (Gauch, 1973). Several studies have demonstrated that Al-toxicity induced symptoms similar to those of P-deficiency (Clarkson, 1967; Edwards *et al.*, 1976; Foy and Brown, 1963) and Ca-deficiency (Edwards and Horton, 1977; Johnson and Jackson, 1964; Foy *et al.*, 1969).

It was reported that plants often suffer from Al-toxicity, if Al concentrations in the soil solution is more than 1 to 2 ppm (Coleman *et al.*, 1968; Ragland and Coleman, 1969), leaf symptoms of Al-toxicity were encountered with 25 ppm in solution (Howler and Cadavid, 1976), pearl millet was not affected by Al levels as high as 16 ppm, while oat root was seriously affected by only 1 ppm Al in the nutrient solution (Long *et al.*, 1973), and marginal and veinal necrosis in deciduous plants was typical Ca-deficiency (Davidson, 1941). In the present study Al-toxicity symptoms took place at the concentrations of more than 100 ppm Al in the kidneybean and buckwheat leaves. The early stage of Al-toxicity was characterized by marginal chlorosis that later developed into necrotic areas extending along the veins toward the midrib; because Al and K_2PO_4 complex settled out to the bottom of the reservoir of culture solution, the Al concentration of culture solution was too low to cause the foliar symptoms as the previous report (Edwards *et al.*, 1976). By P-deficiency the old leaves became chlorotic, but newly formed leaves became dark-green and contained a high concentration of

anthocyanin (Gauch, 1973) and Ca-deficient leaves became chlorotic, rolled and curled (Noggle and Fritz, 1976).

Dry Weight The total dry weight of plant treated with 100 ppm Al contained 50 ppm Ca was slightly decreased by 28% in kidneybean and by 33% in buckwheat (Fig.1). The decrease in dry weight by Al-surplus was presumably due to Ca-deficiency and P-deficiency induced by Al-surplus (Etherington, 1976; Russel, 1973; Wright, 1943). It has been reported that Ca-uptake by wheat seedlings was impaired by aluminum (Johnson and Jackson, 1964) and Al-toxicity in peaches may be related to the reduction of Ca-uptake rate (Edwards and Horton, 1977). In the present experiment the low concentrations of Al (below 10 ppm) contained 50 ppm Ca increased the dry weight of kidneybean and buckwheat (Fig.1). It has been reported that the low concentration of Al stimulated growth in chlorella, lemon and orange cuttings (Gauch 1973).

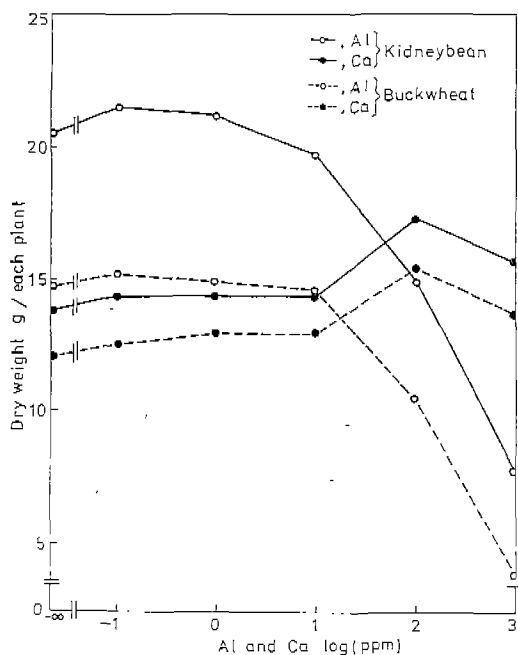


Fig. 1. The total dry weight of kidneybean and buckwheat plants grown by sand culture of various concentrations of Al and Ca for a month. Significant at 5% level in 1,000 ppm Al.

Chlorophyll a and b Chlorophyll a and b was decreased by 30 to 40% in the two plants by Al-toxicity of 100 ppm. (Figs. 2 & 3). As Al concentration was increased, the uptake rates of P, Ca and Mg were decreased (Edwards and Horton, 1977). Magnesium is required as a component of chlorophyll (Noggle and Fritz, 1976). Chloroplasts contain a calcium-activated, light dependent ATPase, and an enzyme isolated from plant cell walls requires both magnesium and calcium (Bonner and Varner, 1976). It was assumed that the decrease of chlorophyll content in both plants might be due to the inhibition of Mg-uptake and enzyme activity by Al-toxicity (Sanchez, 1972). In the present study the chlorophyll a and b content in both plants was highly reduced by supply with low Ca (50 ppm) and high Al (1,000 ppm) concentrations, but it was increased by supply with low Al and high Ca concentrations (Figs. 2 & 3). It has been believed that the chlorophyll a and b contents depend on the ratio of molecular equivalency of Al to Ca in culture solution. When the amount of Al approached to the molecular equivalency of Ca, the content of chlorophyll a and b was almost similar to that of control.

Respiration Respiration by kidneybean supplied with 10 ppm Al, even together with 50 ppm Ca, was decreased by 20%, whereas it was stimulated in buckwheat supplied with 100 ppm Al contained 50 ppm Ca. In the present study the effect of Al on respiration in the two plants was different with each other as the previous report (Russel, 1973). The inhibition of respiration by heavy metals was reported previously (Sung, 1979). It is likely that buckwheat might be more tolerable than kidneybean to Al-toxicity (Fig. 4).

ATP Content With the application of 10 ppm Al contained 50 ppm Ca, ATP content was significantly increased in buckwheat but decreased by 40% in kidneybean. With the application of 100 ppm Al contained 50 ppm Ca, the ATP content was markedly decreased by 50% in buckwheat and by 62% in kidneybean (Fig. 5). The ATP content increased in both kinds of plant leaves in higher Ca concentration, while it decreased in higher Al concentration. The most significant toxic effect of

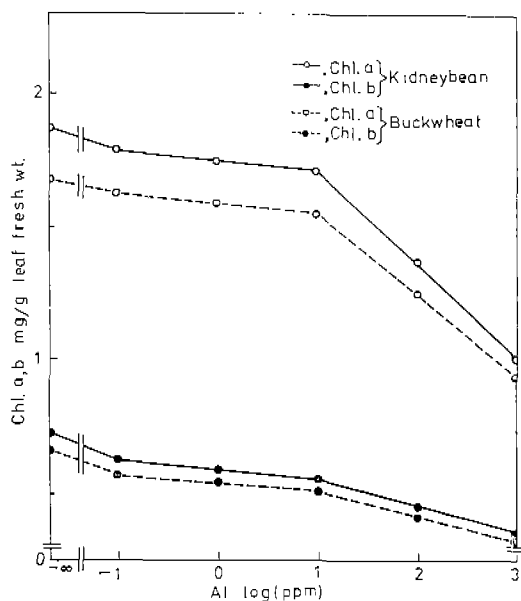


Fig. 2. Chlorophyll a and b content of the leaves in kidneybean and buckwheat plants grown by sand culture of various concentrations of Al for a month. No significance among Al concentrations.

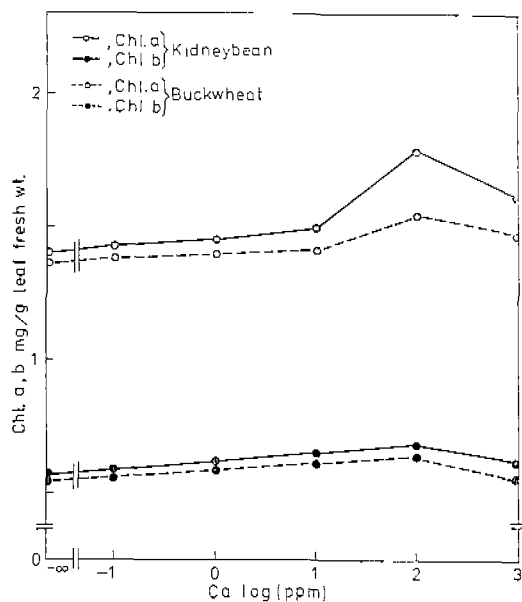


Fig. 3. Chlorophyll a and b content of the leaves in kidneybean and buckwheat plants grown by sand culture of various concentrations of Ca for a month. No significance among Ca concentrations.

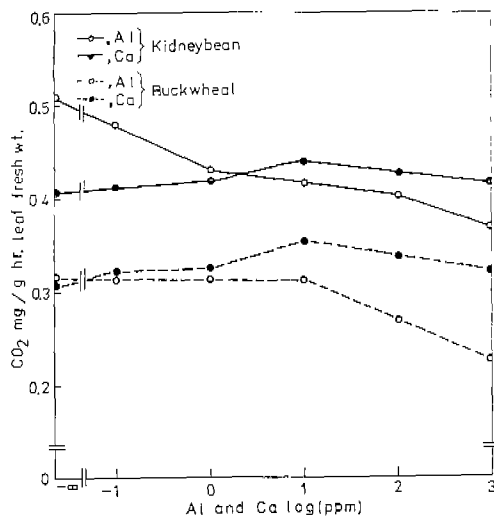


Fig. 4. The respiration of the leaves in the kidneybean and buckwheat plants grown by sand culture of various concentrations of Al and Ca for a month. No significance among Al or Ca concentrations.

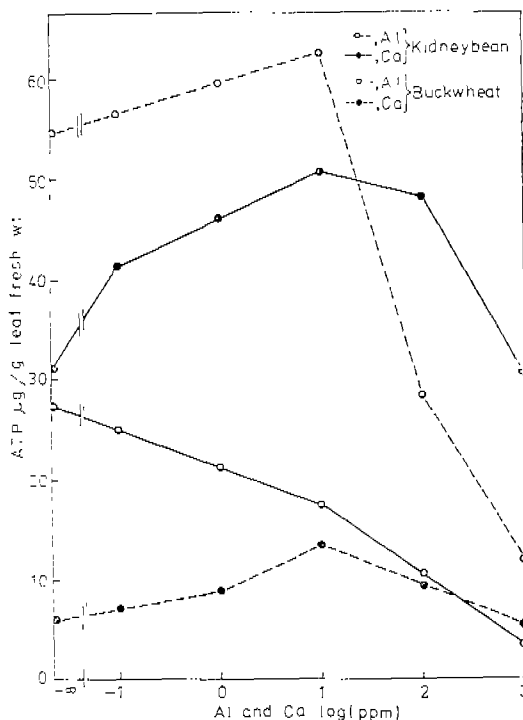


Fig. 5. ATP content in the leaves of kidneybean and buckwheat plants grown by sand culture of various concentrations of Al and Ca for a month. Significant at 1% level among Al concentrations.

Al complexes was previously reported in the impaired phosphorylation reducing both ATP and Co-A levels in animal tissues (Venugopal and Lucky, 1978). Aluminum inhibits acid phosphatase and ATPase activity (Takahashi, 1974). In the present study it was likely that the Al-surplus induced Ca-deficiency and P-deficiency, and therefore the decrease in ATP content was due to the inhibition

of ATP metabolism by Ca- and P-deficiency which is induced by Al-surplus.

Table 1. The average level of ATP content measured at intervals of three hours for a day in the leaves of plants grown with Ca and Al treatments for a month

Supply	Leaves	
	ATP(µg/g)	
	Kidneybean	Buckwheat
Control	10.37	8.29
-Ca	2.94	0.78
+Ca 100 ppm	16.35	11.65
-Al 100 ppm	7.09	1.66
Mean	9.19	5.60
Significance	1% < p < 5%	p < 5%

Rhythm of ATP Level From the determination of ATP content in leaves at intervals of three hours for a day, it could be assumed that there was a certain rhythm of ATP level in both plants. These rhythms showed certain uniformity without being affected by light intensity or temperature in the greenhouse (Figs. 6, 7 & 8). The ATP level of the rhythms in Al-surplus and in Ca-deficiency leaves was somewhat lower than that of control (Figs. 7 & 8). By Al-toxicity of 1,000 ppm average ATP content was depressed by 35% in kidneybean leaves and by 80% in buckwheat leaves, and by Ca-deficiency it was decreased by 72% in kidneybean and by 90% in buckwheat (Table 1).

It has been reported that low temperature did not affect mitochondrial phosphorylation (Lyons and Raison, 1970; Pomeroy and Andrews, 1975)

Table 2. Correlation(r) between the rhythms of ATP level and the variations of temperature(°C) or light intensity (lux) of sun light under the greenhouse conditions during day and night

Plants	Temperature		Lux	
	r-Value	Significance	r-Value	Significance
Kidneybean				
Control	+0.277	none	-0.481	none
-Ca	-0.365	none	-0.558	none
100 ppm Ca	+0.339	none	-0.671	none
100 ppm Al	+0.025	none	+0.561	none
Buckwheat				
Control	-0.074	none	+0.644	none
-Co	-0.099	none	-0.214	none
100 ppm Ca	+0.021	none	+0.561	none
100 ppm Al	+0.260	none	+0.317	none

and it increased ATP content (Sobczyk and Alina, 1978). In the present study the rhythm of ATP level was not affected by temperature changes ranging from 24 to 30°C and by the changes of the light intensity from 50 to 15,000 lux under the greenhouse conditions (Figs. 6, 7 & 8). The circadian rhythm of bioluminescence has reported recently (Kiessig *et al.*, 1979). In the present study the clock cycle of rhythm was found as the

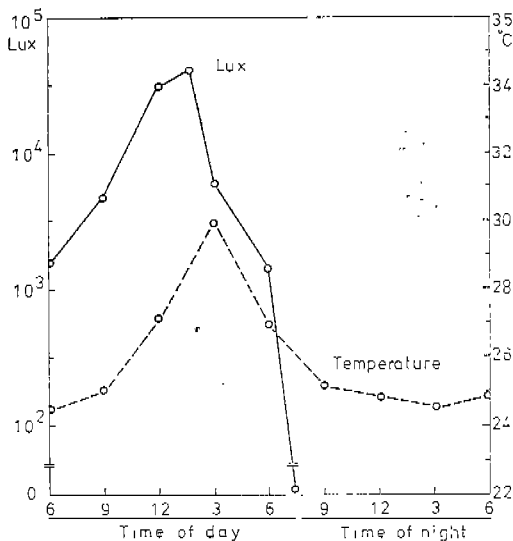


Fig. 6. The greenhouse conditions of sampling with intervals of three hours for measuring of ATP content in plant leaves.

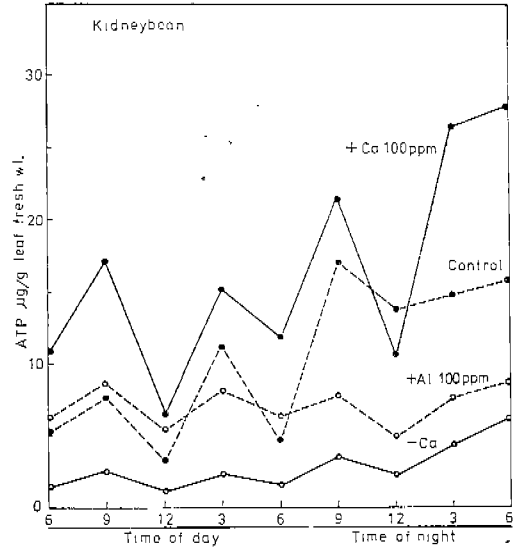


Fig. 7. The rhythm of ATP level in the leaves of kidneybean plant determined at intervals of three hours for a day. Significant at 5% level among the four groups.

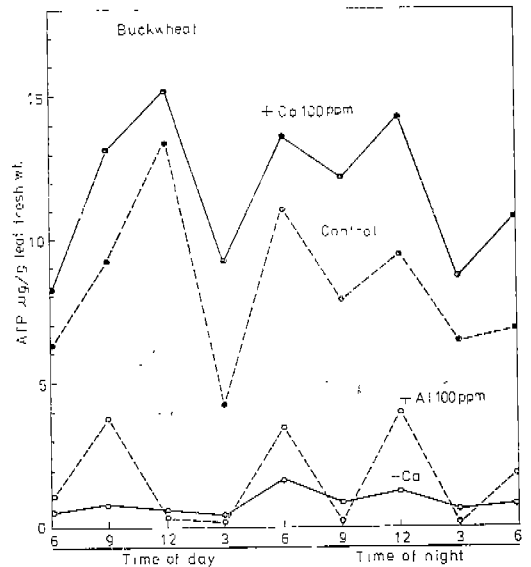


Fig. 8. The rhythm of ATP level in the leaves of buckwheat plant determined at intervals of three hours for a day. Significant at 5% level among the four groups.

previous report (Salisbury and Ross, 1979). It was thought that the period of rhythm in ATP level might be controlled by a single gene as reported in the case of bioluminescence in *Gonyaulax* (Kie-ssig *et al.*, 1979; Salisbury and Ross, 1979; Swc-

Table 3. Temperature and light intensity in the field farm of the four plants for measuring the rhythms of ATP level

Time	Temperature(°C)	Lux
6 : 00	22	500
8 : 00	24	1,000
10 : 00	29	10,000
12 : 00	30	13,000
14 : 00	31	14,000
16 : 00	33	11,000
18 : 00	30	1,500
20 : 00	26	100
22 : 00	24	0
24 : 00	22	0
2 : 00	21	0
4 : 00	22	0
6 : 00	23	100

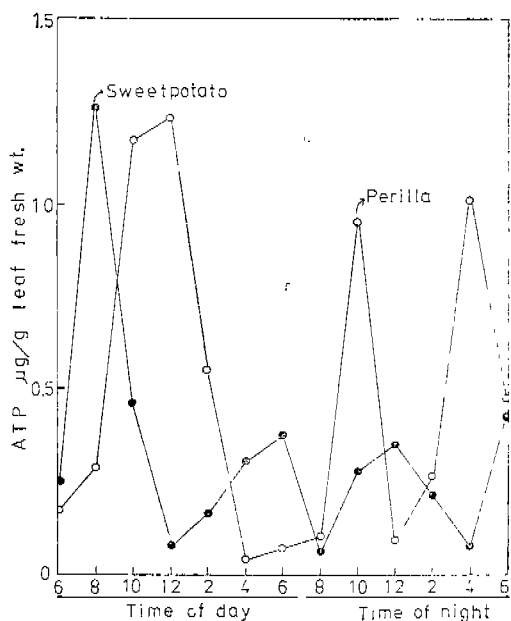


Fig. 9. The rhythm of ATP level in the leaves of sweet potato and perilla plants grown in the field determined at intervals of two hours for a day.

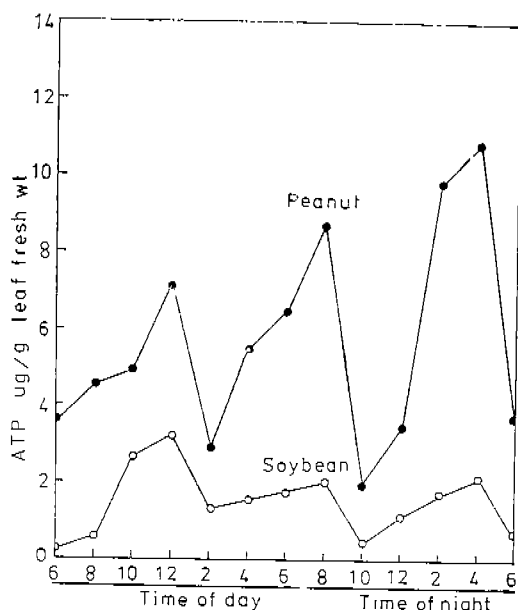


Fig. 10. The rhythm of ATP level in the leaves of peanut and soybean plants grown in the field determined at intervals of two hours for a day.

Table 4. Correlation(r) between the rhythms of ATP level and the variations of temperature(°C) or light intensity (lux) of sun light in the field farm of the four plants

Correlation	Sweet potato	Perilla	Peanut	Soybean
Total ATP, µg/g	4.24	6.37	73.00	19.25
Mean ATP	0.33	0.49	5.62	1.48
r-Value(ATP & °C)	-0.139	+0.116	+0.117	+0.430
Significance	none	none	none	none
r-Value(ATP & lux)	-1.089	+2.141	-0.814	+1.509
Significance	p<1%	p<1%	p<1%	p<1%

eny, 1979). However the effect of Al on the rhythm of ATP level could not be ascertained in this study. In order to confirm the rhythm of ATP level we examined leaves of four other kinds of plants such as sweet potato, perilla, peanut and soybean grown normally for two months in the field.

In any case, the rhythm of ATP level was not affected by light intensity or temperature condition. Therefore we concluded that the rhythm of ATP might be controlled by the heredity factor.

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摘 要

강남콩(*Phaseolus vulgaris* L.) 및 메밀(*Fagopyrum esculentum* Mönch)의種子를 모래를 넣은花盆에播種하여 Hoagland solution으로 2週間 砂耕栽培하였다. 이植物은花盆에서 8個體씩 남기고 추운後 여기에 Al 및 Ca를 다음과 같이處理하였다. Al 및 Ca의濃度는 Hoagland solution으로 各各 0~1,000 ppm에서 6個區를 만들고, Al區에는 50 ppm Ca를, Ca區에는 100 ppm Al을添加한 것을培養液으로 하였다. 이培養液을 2日 間隔으로 300 ml씩 1個月間 處理하여 材料植物을 生長시킨 後 葉을 採取하여 測定材料로 하였다.

Al過剩은 그 症狀이 Ca缺乏症과 類似하였으며 강남콩의 境遇, 葉脈에서 黃褐色 斑點이 나타나 漸次 擴大되었고 葉은 早期 脫落되었다. 메밀의 境遇는 葉 가장자리에서 necrosis 症狀을 나타내었다. Chlorophyll의 含量은 Ca濃度의 二倍 以上인 Al濃度區에서 30%以上 減少되었다. Al有毒症狀의 感受性은 메밀보다 강남콩이 더욱 높았다.

두 植物葉의 ATP含量은 control에 比하여 100 ppm Al 過剩에서, 강남콩의 境遇 32%, 메밀의 境遇 80% 減少되었고, Ca缺乏에서, 강남콩의 境遇 72%, 메밀의 境遇 90% 減少되었다. 하루동안에 3時間마다 測定한 葉中 ATP의 含量趨勢를 調査한 結果 溫室條件下에서 照度와 溫度에 關係없이 ATP水準에 一定한 rhythm이 있음을 發見할 수 있었다. Al過剩 및 Ca缺乏區에서의 rhythm은 낮은 ATP含量的 範圍에서 나타났다. 野外 農作物 4種의 境遇 ATP水準의 rhythm은 溫度和 關係없었으나 낮 동안에는 햇빛의 照度和 有意性 있는 相關을 나타내었고 밤에는 照度和 關係없이 rhythm이 있었다.

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