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Effect of temperature and light on foliar absorption of P and Rb by Chrysanthemum and Pilea *

SZCZEPAN MARCZYŃSKI [1] and H. B. TUKEY, Jr. [2]

[1] Faculty of Horticulture Warsaw Agricultural University, ul. Nowoursynowska 166, 02-766 Warszawa, Poland
[2] University of Washington, Seattle, WA, USA

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Abstract

Young plants of *Pilea cadierei* Gagnep Guillaum and *Chrysanthemum morifolium* Ramat. 'Giant # 4 Indianapolis White' were grown in Hoagland's solution in growth chambers. Their leaves were treated with rubidium phosphate double labelled with ^{33}P and ^{86}Rb. Light intensity, period of pretreatment in light or dark, daylength, and air temperature had different influences on foliar uptake of each ion, as did plant species and leaf surface. With all variables tested, uptake and translocation of Rb was much greater than of P. Absorption of both P and Rb through the lower surface was as much as 8 times greater than through upper surface, especially with *Pilea*. Light had a greater effect upon uptake of both P and Rb by *Chrysanthemum* than by *Pilea*, but did not influence uptake as much as previously reported.

INTRODUCTION

The influence of environmental factors on foliar penetration and translocation of K and P is not understood clearly, despite many reports in literature (Barrier and Loomis, 1957; Greene and Bukovac, 1971; 1972; Marczyński and Jankiewicz, 1978, Sargent and Blackman, 1962; Teubner et al., 1957; Thorne, 1958). This has, in part, limited commercial use of foliar nutrition with horticultural crops. Therefore, research was conducted to determine the

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influence of light and air temperature on the uptake and translocation of P and Rb by plant leaves, with Rb used as a tracer of K (Hafez and Rainz, 1972).

MATERIALS AND METHODS

Cuttings of *Chrysanthemum morifolium* cv. 'Giant # 4 Indianapolis White' and *Pilea cadierei* were rooted under intermittent water mist for 2 weeks, until roots were 1.0-1.5 cm in length. Cuttings were uniformly graded and, after washing the roots, were grown in a greenhouse in aerated Hoagland's nutrient solution containing half-strength P and K until 2-3 new leaves had developed in about 7 days.

Plants were placed in growth chambers and allowed to equilibrate for 1 day before treatment. Certain factors were kept constant unless otherwise stated: day-night temperature 22°C± 1°, relative humidity 65%± 2.5%, light intensity 20×10^3 lx$\pm1\times10^3$ lx, a 16-h day, with treating in the middle of the day.

A dosing solution was labelled with 1.5 μCi $H_3{}^{33}PO_4$ (carrier-free) and 0.15 μCi ^{86}RbCl per 20 μl of 10 mM rubidium phosphate buffered with phosphate buffers at pH 7.5 with no surfactant. In experiments with high light intensity and different times of treatment, plants were treated with 25 mM rubidium phosphate with 0.1% Ethonid 0/15 as a surfactant.

The upper or lower leaf surface was treated with a 20 μl droplet of dosing solution without surfactant placed directly on the leaf surface. Before treatment of the lower surface, the leaves were carefully reversed while still attached to the plant and fixed in position by wire holders; this manipulation had no effect upon the results (Fig. 1) but made treatment much easier. If the dosing solution contained surfactant, it was pipetted into plastic rings of 7 mm internal diameter and 3 mm in height, fixed to the leaf surface with vaseline. The radioactive treating solution remained within the ring; the vaseline on the outside part of the ring had negligible radioactivity 48 h after treatment. For comparison, rings were fixed to the leaf surface with silicone rubber, but injury occured. At the end of the treating period, generally 48 h, a 1. 35 cm — diameter, disk encompassing the treated area of the leaf was removed with a cork borer. The remaining plant parts were dried at 100°C and ashed for 12 h at 525°C in a muffle furnace. After cooling, the ash was dissolved in 5 ml of 6 N HCl and evaporated to dryness on a hot plate. After cooling 5 ml of 1 N HCl were added to redissolve the ash, and 0.5 ml aliquots of the solution were assayed for radioactivity using a scintillation counter. Corrections were made for background and quenching.

In some experiments, the disks punched from *Pilea* leaves were washed with 50 ml of 1 M K_2HPO_4 and 50 ml of water. Total uptake was the sum of the radioactivity in the disks and that translocated to other parts of the plant. Radioactivity which was translocated from the treatment disk was called absorption and translocation radioactivity. Because *Chrysanthemum* leaves were covered with trichomes which made them difficult to wash, the disks punched out from these leaves were discarded and not counted.

Stomatal and trichome density were determined with a silicone rubber impression technique (Z e l i t c h, 1961); stomatal opening was determined with a Lambda auto-porometer LI-65.

Each treatment had 5-10 replications. All experiments were repeated twice. Data after angular transformation were subjected to analysis of variance and Tukey's W-procedure was used for comparing treatment means (S t e e l e and T o r r i e, 1960).

RESULTS

Both surfaces of *Chrysanthemum* leaves were covered with the same type of trichome but of different densities. Density on the upper surface of the third leaf from the apex was 1540 trichomes/cm² while on the lower surface it was approximately twice as dense. On both surfaces

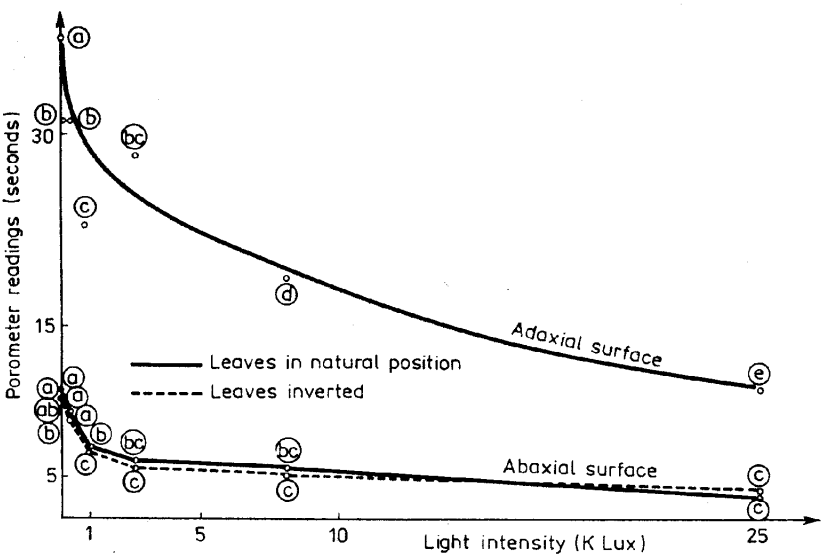

Fig. 1. Effect of light intensity on stomatal opening of *Chrysanthemum* leaves. Means on each curve designated by the same letter do not differ significantly at P=0.01

the highest trichome density was over a main vein at the base of the leaf. Approximately 6070 stomata/cm² were found on the upper surface while on the lower surface the density was about 2-2.5 times greater. Stomatal density was greater in the middle part of the leaf than on the edges.

On the lower surface of *Chrysanthemum* leaves, stomatal opening increased with increasing light intensity up to 2700 lx, especially up to

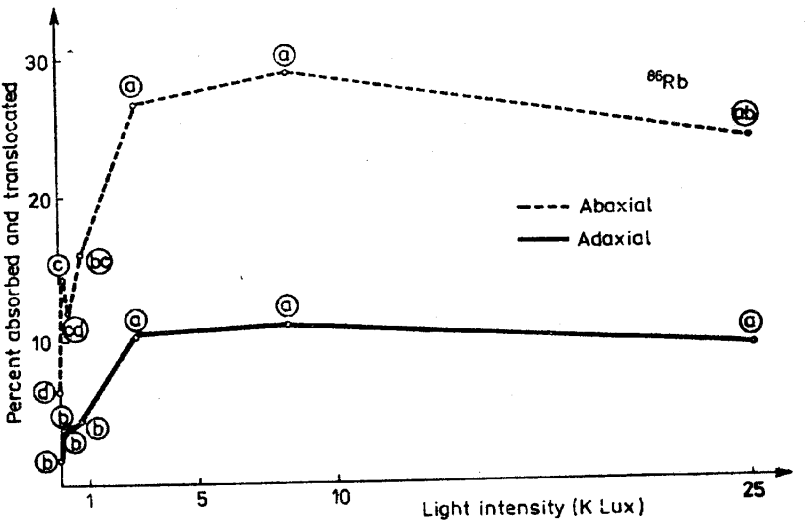

Fig. 2. Effect of light intensity on absorption and translocation of ^{86}Rb with 25 mM rubidium phosphate with 0.1% Ethonid by *Chrysanthemum* leaves. Means designated by the same letter do not differ significantly at P=0.01

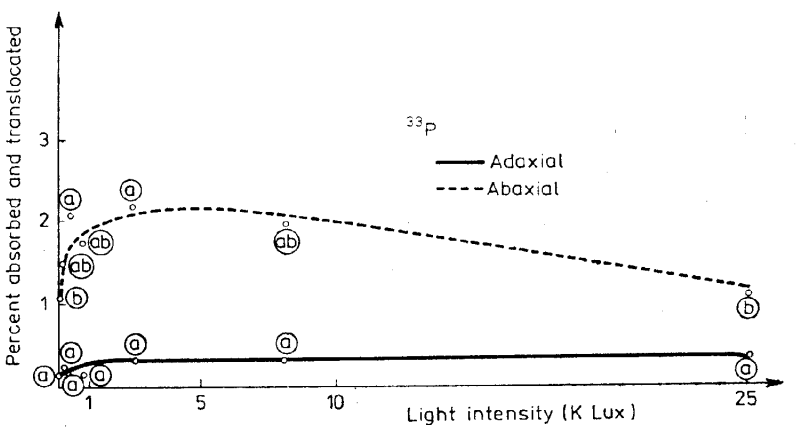

Fig. 3. Effect of light intensity on absorption and tranlocation of ^{33}P with 25 mM rubidium phosphate with 0.1% Ethonid by *Pilea* leaves. Means designated by the same letter do not differ significantly at P=0.01

900 lx (Fig. 1). On the upper surface there was a continuous increase in stomatal opening between darkness and 25 000 lx.

The surface of *Pilea* leaves was smooth with no trichomes. No stomatas were seen on the upper surface, whereas about 13×10^3 stomata/cm^2 were dispersed uniformly on the lower surface. Stomata on the lower surface of *Pilea* leaves opened with light of 100 lx. Increasing the light intensity to 2700 lx caused a trend toward larger stomatal opening but differences were not statistically significant; increasing light intensity to 25 000 lx had no further effect, similar to *Chrysanthemum*. Cn the upper surface, porometer readings taken in darkness were 103 s, while during the day readings ranged between 40 and 65 s, but this was not correlated with light intensity.

In all experiments, total P uptake through the adaxial leaf surface of *Pilea* was 5-15 times lower than through the abaxial surface and ranged between 2.8% and 11.5% of the applied phosphorus absorbed after 48 h (data not shown). Most of the activity remained in the treated disk; only 2-10% of the nutrient taken up was translocated to other, parts of the plant (Fig. 2). Uptake of Rb was 3 times greater through the lower leaf surface of *Pilea* than through the upper. In *Chrysanthemum* leaves the difference in uptake between surfaces was smaller. When a surfactant was added to the dosing solution, uptake and translocation was greater through the abaxial than the adaxial surfaces (Fig. 3). No distinct difference in uptake between surfaces was usually noted when the surfactant was not used (Tables 1, 2).

Table 1

Effect of time of treatment during the day and night on absorption and translocation of 25 mM rubidium phosphate with 0.1% Ethonid by *Chrysanthemum* leaves. Plants were harvested 48 h after treatment

Time of treatment	^{33}P		^{86}Rb	
	treated surface			
	adaxial	abaxial	adaxial	abaxial
2 h before light	0.9 a	1.8 b	15.5 a	17.6 ab
- at the moment of turning on the light	1.4 a	2.3 ab	15.5 a	18.0 ab
2 h in the light	1.3 a	2.5 ab	14.5 a	21.1 ab
8 h in the light	1.4 a	3.5 a	13.1 a	17.1 b
14 h in the light	2.0 a	2.3 ab	18.4 a	23.8 a
- at the moment of turning off the lihgt	1.2 a	2.9 ab	15.8 a	20.6 ab
2 h in the dark	1.1 a	2.9 ab	12.5 a	22.7 ab

Means within a column followed by a different letter are significantly different at P = 0.01.

Table 2

Effect of the day lenght on % absorption and translocation of 10 mM rubidium phosphate by *Pilea* and *Chrysanthemum* leaves for 48 h

Day length	^{33}P				^{86}Rb			
	total absorbed		absorbed and translocated		total absorbed		absorbed and translocated	
	adaxial surface	abaxial surface	adaxial surface	abaxial surface	adaxial surlace	abaxial surface	adaxial surface	abaxial surface
Pilea								
Dark	7.4 a	69.1 ab	0.40 a	4.2 b	15.8 b	71.6 a	13.1 b	50.3 a
8 h	3.3 a	84.0 a	0.12 a	6.9 a	23.4 ab	77.7 a	18.2 ab	64.3 a
16 h	10.9 a	73.5 ab	0.19 a	5.5 ab	31.7 ab	70.6 a	23.4 ab	62.0 a
24 h	8.4 a	37.9 b	0.28 a	3.5 b	33.2 a	67.2 a	29.2 a	60.1 a
Chrysanthemum								
Dark			1.3 b	0.7 b			39.2 b	58.4 a
8 h			3.4 a	2.1 ab			71.1 a	55.5 a
16 h			2.9 ab	3.3 a			64.8 a	61.9 a
24 h			2.7 ab	2.3 ab			43.0 b	72.7 a

Means within a column followed by a different letter are significantly different at P = 0.01.

Uptake through both surfaces of *Chrysanthemum* increased as light intensity increase (Fig. 3). In the case of the lower surface, significantly greater uptake and translocation of ^{86}Rb occured even at 100 lx as compared with darkness. Influence of light intensity on uptake was noticed to 2700 lx. Further increase in light intensity to 25 000 lx did not change uptake.

Results with *Pilea* were similar qualitatively, but not quantitatively. The uptake of ^{86}Rb averaged 5% of the radioactivity applied for upper surfaces and 10-15% for lower surfaces, and increases in light intensity from 300 to 25 000 lx caused a small but statistically significant decrease in absorption and translocation by abaxial surface (data not shown). Further, there was a statistically significant influence of light intensity on the uptake of ^{33}P by the abaxial surfaces although the trend was similar to *Chrysanthemum* leaves (Fig. 4).

Plants growing under a 16-h day 8-h night were treated at different times to determine when darkness had the greatest inhibitory influence on uptake. Because the radioactive treating droplet dried in about 2 h plants were treated the moment lights were turned either on or off, 2 h before and 2 h after, or in the middle of the day. There was no clear difference among the treatments (Table 1) in the quantity of ^{86}Rb and ^{33}P absorbed and translocated, probably because the change in concentration of the ion in solution as the droplet dried had a greater influence than did the time of treatment. This suggested that total time

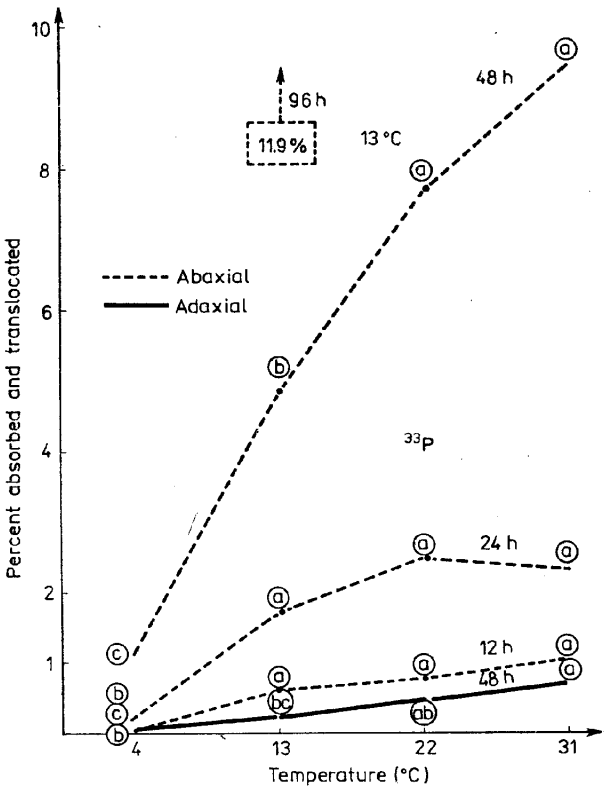

Fig. 4. Effect of temperature on absorption and translocation of ^{33}P with 10 mM rubidium phosphate by *Pilea* leaves. (During 12, 24, 48, 96 h after treatment). Means designated by the same letter do not differ significantly at P=0.01

of exposure to light during the absorption period even after drying of the droplet was more important than time of treatment. To check this, when plants were treated under different day lengths (Table 2), more ^{33}P was absorbed and translocated through the abaxial leaf surface of *Pilea* under an 8-h day than in darkness; there was decreased absorption with further increase in day length. Similarly, *Chrysanthemum* leaves had greater absorption and translocation of ^{33}P in an 16-h day than in darkness, but there were no differences with varying day lengths (Table 2). Day length did not influence the uptake of ^{86}Rb by the lower surface of *Pilea* or *Chrysanthemum*. In the case of the upper surface, greater uptake in *Pilea* occured under constant light, and *Chrysanthemum* under the 8- and 16-h day.

In all experiments, as the temperature increased from 4 to 22°C, absorption and translocation of ^{33}P and ^{86}Rb through both surfaces of *Pilea* and *Chrysanthemum* leaves increased, usually linearly (Figs. 5, 6; data for ^{86}Rb not shown). However, absorption and translocation of

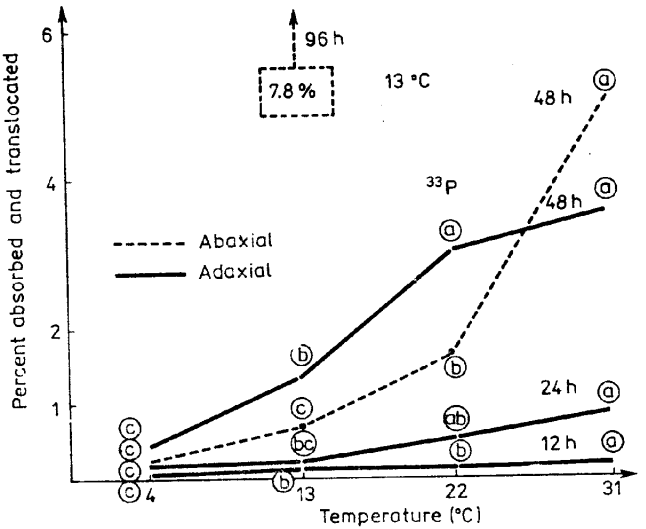

Fig. 5. Effect of temperature on absorption and translocation of ^{33}P with 10 mM rubidium phosphate by *Chrysanthemum* leaves. (During 12, 24, 48, 96 h after treatment). Means on each curve designated by the same letter do not differ significantly at P=0.05

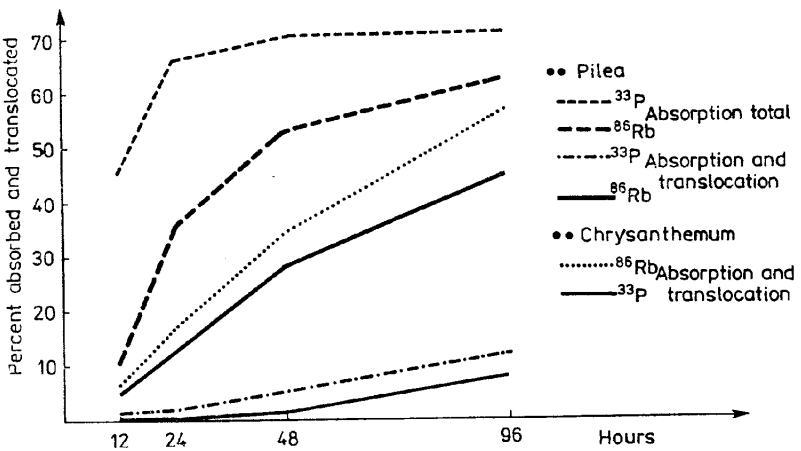

Fig. 6. Time-course of absorption and translocation of ^{86}Rb and ^{33}P with 10 mM rubidium phosphate by abaxial *Pilea* and adaxial *Chrysanthemum* leaf surface

^{86}Rb by the upper surface of *Pilea* leaves was greatest between temperatures of 13°C and 22°C.

Temperature coefficients (Q_{10}) ranged from 1 to 10, usually between 1.5 and 5.0. Uptake of P and Rb by both surfaces of *Pilea* leaves at 13°C increased with time, but at a decreasing rate, such that uptake

between 48 and 96 h after treatment showed no differences (Fig. 2). At the same time, absorption and translocation of ^{33}P and ^{86}Rb outside the treated spot increased significantly (Figs. 2, 5). Even greater change in absorption and translocation of P was seen in *Chrysanthemum* plants, with a nearly five-fold increase between 48 and 96 h (Fig. 6). Absorption and translocation of ^{86}Rb by *Chrysanthemum* leaves increased uniformly with time (Fig. 2). The *Pilea* plants absorbed ^{86}Rb and ^{33}P in similar quantities, but Rb was translocated from the treated area more rapidly; after 48 h, 4-10 times more rubidium was translocated than phosphorus.

Once absorbed, P and Rb were translocated to all plant parts as the temperature increased. In *Pilea*, more ^{33}P and ^{86}Rb were translocated to the roots and the stems and leaves basipetal to the treated leaf, and less were found in the stems and leaves acropetal to the treated leaf (Fig. 7; data for ^{86}Rb not shown). In *Chrysanthemum*, lesser amounts of ^{33}P and ^{86}Rb were translocated to the roots, and greater amounts were translocated acropetally from the treated leaf (Fig. 8; data for ^{86}Rb not shown).

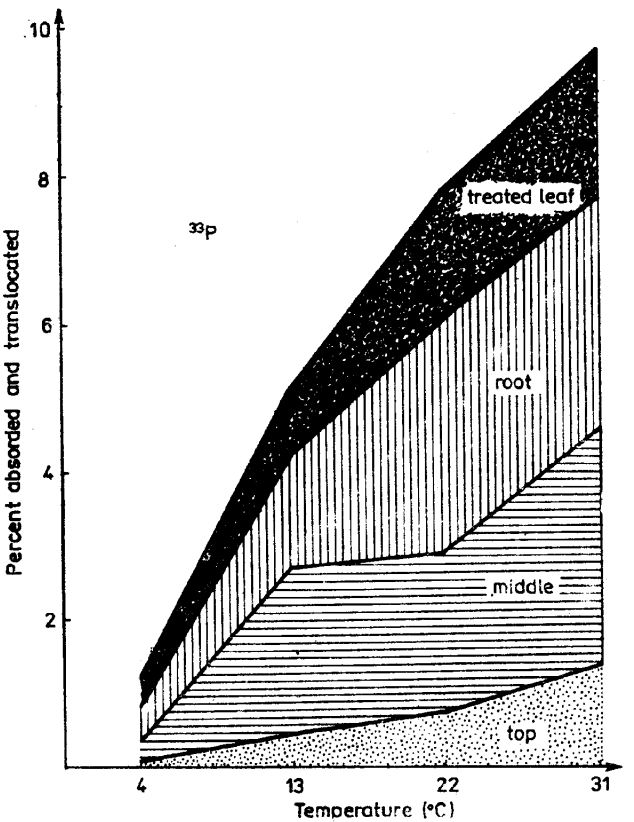

Fig. 7. Effect of temperature on absorption and translocation of ^{33}P with 10 mM rubidium phosphate to different parts of *Pilea*

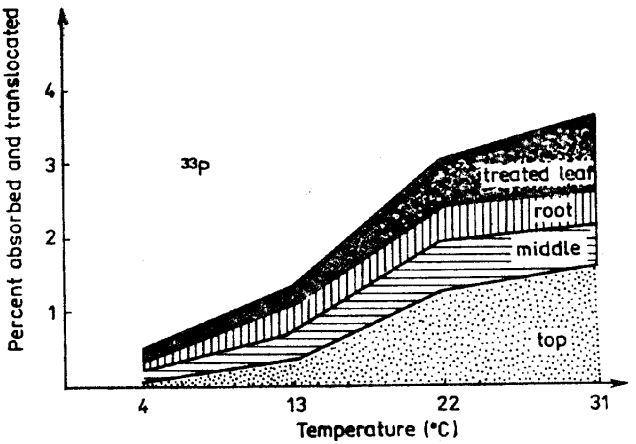

Fig. 8. Effect of temperature on absorption and translocation of ^{33}P wit 10 mM rubidium phosphate to different parts of *Chrysanthemum*

DISCUSSION

Light and air temperature had different influences on the uptake of both Rb and P ions, as did plant species and the leaf surface treated.

The small amount of phosphorus absorption by the upper as compared with the lower surface of *Pilea* leaves does no seem to be conditioned by cuticle thickness, because the cuticle on both surfaces is thin (P a p a r o z z i, 1978). However, there may be differences in the structure of epicuticular wax between the two surfaces which may cause differences in absorption as was noted in other species (L e e c e, 1976; R e e d, 1979). More likely, the differences in P absorption are related to the absence of stomata on the upper surface; the relationship between stomatal density and absorption by some plant species was noted before (J a c o b y, 1975; J y u n g et al., 1965). There was also greater absorption of Rb when stomata were present, but the differences in Rb absorption between leaf surfaces was less than with P. This could be related to the negative charge of the cuticle, which allowed easier absorption of cations that anions.

When surfactant was added to the dosing solution (Fig. 3), there was a distinct relationship between stomatal density and absorption in both leaf surfaces of *Chrysanthemum*. When the solution did not include a surfactant (Table 2), no relationship was shown. This is most likely due to differences in trichome density between *Chrysanthemum* leaf surfaces. However, absorption may occur by the base part of trichomes (H u l l, 1970), but the trichomes may inhibit contact between the treating solution and the leaf surface, unless a surfactant is used.

Light can influence leaf absorption in different ways. It has been suggested that the primary light effects is on build-up of carbohydrates in the leaves (Ahlgren and Sudia, 1966; Greene and Bukovac, 1971; Sargent and Blackman, 1969). Our results did not support this, for at higher light intensities at which assimilation occurs, absorption and translocation did not change. Others have suggested that light did not influence foliar absorption by changes in photosynthesis because uptake was not related to CO_2 presence (MacDonald and MacLeod, 1975; Middleton and Sanderson, 1965). Light could influence cytoplasmic permeability and active transport (Lauchli, 1972) and in this way could change leaf absorption. Also an increase of permeability of the cuticular membrane on the guard cells when stomata are open, as was suggested by Schönherr and Bukovac (1978), may enhance leaf absorption. This agreed in general with our results, for low light intensity was correlated with absorption through the lower surface of *Pilea* leaves with many stomata, until stomata were fully open, after which further increases in light intensity had no effect. Also in the lower surface of *Chrysanthemum* leaves, a strong correlation was found between absorption and stomatal opening. However, on the upper surface where stomata are open less in light, the correlation occurred but was not as marked.

Increasing day length caused progressive increase in Rb absorption by the upper surface of *Pilea* leaves, probably by an effect upon stomatal opening. However, it is difficult to explain greater uptake of P by the lower *Pilea* leaf surface and Rb by the upper *Chrysanthemum* leaf surface under an 8-h day in comparison with continuous light.

Treatment at different time of day did not have a great influence upon absorption and translocation, although previous reports showed the greatest absorption when plants were treated in the morning (Teubner et al., 1957; Thorne, 1958).

Increasing the temperature from 4 to 31°C greatly increased foliar absorption of ^{33}P and ^{86}Rb and translocation to other plant parts, which agrees with most earlier reports (Greene and Bukovac, 1971; 1972; Marczyński and Jankiewicz, 1978; Sargent and Blackman, 1962; van Overbeek, 1956) but not all (Barrier and Loomis, 1957; Middleton and Sanderson, 1965). The greater increase in absorption at lower temperatures (4-22°C) than at higher temperatures (22-31°C) may be due to increased cohesion of fatty substances of plasmatic membranes under lower temperatures (Van den Horent and Hooymans, 1955) or by changes in cuticular permeability due to changes in wax structure (van Overbeek, 1956).

Absorbed P and Rb moves out of the treated spot uniformly with

time. Both were translocated to all plant parts, as was reported (Asen et al., 1953; Levi, 1970; Thorne, 1958) dependent upon temperature and metabolic activity of the plants. In young plants, P and Rb were translocated mostly to the root system of *Pilea* and to the above-ground parts of *Chrysanthemum*. Uptake and translocation of both P and Rb varied between experiments, probably because of differences in physiology and leaf surface development in plants prepared in the greenhouse during different periods of the year (Thorne, 1958).

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Wpływ temperatury i światła na wnikanie P i Rb do liści *Chrysanthemum* i *Pilea*

Streszczenie

Młode rośliny *Chrysanthemum morifolium* Ramat. odmiany 'Giant # 4 Indianapolis White' i *Pilea cadierei* Gagnep Guillaum rosły w hydroponice, w pożywce Hoagland'a, w kamerach wzrostowych. Ich liście traktowano fosforanem rubidu podwójnie znakowanym — ^{33}P i ^{86}Rb. Intensywność światła, okres wstępnego traktowania na świetle lub w ciemności, długość dnia i temperatura powietrza miały różny wpływ na wnikanie do liści każdego z jonów. Wnikanie było również uzależnione od gatunku rośliny i powierzchni liścia. Po uwzględnieniu wszystkich zmiennych występujących w doświadczeniu stwierdzono, że wnikanie i przemieszczanie Rb było znacznie większe niż P. Absorpcja P i Rb przez dolną stronę liści była do 8 razy większa niż przez górną powierzchnię, zwłaszcza u *Pilea*.

Pobieranie P i Rb przez *Chrysanthemum* było bardziej uzależnione od światła niż w przypadku *Pilea*. Wpływ światła na wnikanie do obydwu roślin był jednak mniejszy niż dotychczas sądzono.