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Rapid Growth Responses of *Avena* Coleoptile Segments to Lanthanum and Other Cations

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ABSTRACT

The rapid growth responses of oat (var. Victory) coleoptile segments treated with millimolar concentrations of the chlorides of La^{3+}, Ca^{2+}, K^+, and NH_4^+, respectively, have been measured. La^{3+} and Ca^{2+} initially depressed the endogenous elongation rate. In the case of La^{3+} a prolonged stimulatory effect on the rate of elongation was produced by concentrations of 50 millimolar down to 20 micromolar after an initial depression of elongation rate. The effect of K^+ was slightly stimulatory and showed a synergistic effect in combination with La^{3+}. NH_4^+ produced an immediate rapid increase in elongation rate. La^{3+} did not behave as a "super calcium" in its action upon the spontaneous growth response. The prolonged elongation of the La^{3+}-treated segments exhibiting the spontaneous growth response is apparently a newly observed effect. These rapid growth responses are interpreted as an interaction between anionic lipid-protein complexes in the plasmalemma and the respective ions.

The effects of specific actions on the growth processes of plants have long been of interest to agronomists and plant physiologists. Drobkov (6) used solution culture techniques and demonstrated that yield of pea plants was increased by the addition of 10^{-2} g of lanthanum per vessel. Lundegårdh *et al.* (16) have studied the absorption of chloride salts of the rare earth elements. More recently the botanical quarantine studies of the Apollo Moon Missions demonstrated biological effects of lunar soil (26). Sunflower (*Helianthus annuus* L.) and corn (*Zea mays* L.) were reported to show increased vigor with prominent root development noted for corn. A later report (12) suggested that the stimulation of plant growth observed had its origin in the release of Fe, Ca, and Mg as well as Mn from the lunar soil. It is possible that other factors may have been involved in the growth stimulation effects noted by the Apollo 11 and 12 quarantine investigators. La was detected in the analysis of soil (16.3 μg/g) and rock samples (7.5–29.2 μg/g) from Tranquillity Base (9). The concentrations of the various rare earth elements ranged from 1.5 to 19.7 μg/g in soil and from 1.4 to 84.2 μg/g in the rock samples. It may be that the stimulatory effects noted had as their basis the presence of La and rare earths in the lunar soil.

An inhibitory effect of La^{3+} on the auxin-stimulated elongation of *Avena* coleoptile segments has been reported by Pickard (18). In addition, it was noted that the degree of inhibition by $LaCl_3$ and $CaCl_2$ was very similar.

Other physiological effects of La in plant systems have been reported. Poovaiah and Leopold (19) have shown that Ca^{2+} and La^{3+} decrease the leakiness of beet root cells while NH_4^+ increases leakiness. In another paper (20) they reported increased binding of α-naphthalene-acetic acid to membrane fractions made from corn (*Z. mays* L.) coleoptiles in the presence of La^{3+}, Ca^{2+}, and Mg^{2+}. A slight inhibition of binding was noted in the presence of NH_4^+.

Recent use of La^{3+} as a probe for determining the permeability of tissues (22, 24), the demonstrated effect of this ion on the permeability of plant cell membranes (14), and the inhibitory effect upon auxin-stimulated growth (15) suggested the use of the rapid growth response-measuring apparatus to evaluate the effect of La^{3+} and other ions on the SGR[1] of *Avena* coleoptile segments (8, 27).

MATERIALS AND METHODS

Uniform coleoptiles of *Avena sativa* L. var. Victory were grown as previously described (27). The seed oats were obtained from Svalof, Sweden. The harvest, cutting, and mounting of the coleoptile segments were conducted in dim green light. A 1-cm segment was cut 3 to 4 mm from the tip of each coleoptile. The coleoptiles were selected in pairs to ensure the greatest possible uniformity of biological material. Five of the segments, one of each pair selected, were threaded on a 0.30-mm-diameter plastic monofilament. Each of the filaments was placed in a high resolution growth-recording device similar to those described by Evans and Ray (7) and dela Fuente and Leopold (5). By placing a cam on the external drive shaft of the recorder the length of each column of coleoptile segments can be recorded. A microswitch riding on the cam switches the recorder's input from one transducer-amplifier to the other at 5-min intervals. This twin growth-recording device and the pair selection technique (each comparison made with coleoptiles from the same crop of seedlings) permits the simultaneous measurement of a treatment and its control. This combination of instrumentation and technique makes possible comparisons of growth responses at a high level of precision.

The treatments were supplied in a solution of 2% sucrose, 2.5 mM maleic acid (10), and adjusted to pH 6.0 with NaOH. The experiments were performed at 30 C in a controlled temperature chamber. The treatments consisted of solutions of reagent grade salts of La, K, NH_4, and $CaCl_2$. The particular treatment was applied at 1 or at 3 h from the time of cutting of the coleoptiles. The course of coleoptile elongation was generally recorded for 8 h. Each experiment was done at least twice. The endogenous growth rate (control) and the response to 10 mM $LaCl_3$ at h 1 were done seven and six times, respectively, to permit statistical analysis.

The reproducibility of the results and the validity of using data from experiments done twice was established by: (*a*) the experimental protocol with exhaustive provisions to reduce biological variability by ensuring uniformity of plant tissue which included selection of the experimental material for uniformity at the time of husking, after soaking and pair selection during the harvest of the coleoptiles (see ref. 27); (*b*) the simultaneous comparison of control to experimental treatment; (*c*) extensive replication of

[1] Abbreviation: SGR: spontaneous growth response.

certain experiments to define the variability statistically (Table I). With six or seven replications, it was evident that the hourly rate of elongation was reproducible (rates from 0.52 to 2.60 with 95% confidence limits ranging from as little as ± 0.22 to as much as ± 0.70). The variability between duplicate runs was least in the comparisons between the control and the $LaCl_3$ treatment rates of elongation (Fig. 1A, h 3 control 2.5, 2.5 and 10 mM $LaCl_3$ 0.8, 0.5) and between the control and the $CaCl_2$ treatment rates of elongation (see Fig. 3C, h 6, 10 mM $LaCl_3$ 1.5, 1.5, and 10 mM $CaCl_2$ 0.2, 0.3. The greatest variability was found between the duplicate runs of the 10 mM NH_4Cl treatment (Fig. 3B). At h 2 the rates of elongation were 4.4 and 6.4, a strong stimulatory effect.

The determination of the rate of elongation was accomplished by measuring the angle of the trace on the chart record and referring to this value on the calibration curve *i.e.* a trace departing from the longitudinal axis of the chart paper at 15 degrees indicated a rate of elongation of 2.5 mm/h·column of 10 1-cm segments. In determining the angle, a straightedge was applied over the chart recording coinciding with the lines of the left or right transducer-amplifier trace and the angle was measured with a protractor. At least 30 min of a given hour at a steady rate was required to assign a rate.

In order to avoid disturbing the previously established calibration of the apparatus all reported rates of elongation are on the basis of a 10-cm column of segments.

RESULTS

The treatment with 10 mM $LaCl_3$ immediately depressed the rate of elongation and delayed the SGR (Fig. 1). The SGR of the control column of coleoptiles started at 2 h and 15 min from the time of cutting and began slowing by h 3. The delayed and slowed SGR elongation of the La treatment continued longer than the SGR of the control and exceeded the control in final length at h 10 ($\bar{X}$ = 61 mm versus $\bar{X}$ = 59 mm).

In Figure 1B the treatments with $LaCl_3$ and KCl, each at 10 mM concentration, were not supplied until h 3. With the application of the treatment after the SGR, the increased rate of elongation at h 5 by the La-treated coleoptiles is similar to that observed in Figure 1A. This stimulation of elongation is not an increase in the expression of the SGR.

Combining $LaCl_3$ and KCl each at 10 mM concentration in the treatment solution (Fig. 1C) increased the rate of elongation in comparison with the $LaCl_3$ treatment. The presence of K^+ with La^{3+} lessened the initial inhibition noted for La^{3+} alone and delayed the SGR by 0.5 h.

In Figure 2A the effect on the elongation rate of the column of coleoptiles in the KCl-$LaCl_3$ solution each at 10 mM concentration is compared with the effect of KCl treatment at 10 mM concentration and presents a very different picture than that in Figure 1C. The SGR of the coleoptile segments in the KCl treatment occurred and declined at the same times as did the control (Fig. 1A). At h 4 the combination treatment began to increase in elongation rate and exceeded the elongation of the KCl-treated column of segments by a mean value of 3.2 mm at h 6.

Table I. *Elongation Rates of Avena Coleoptile Segments*

Hour	Control, N = 7							$\bar{X}$
	mm/h·column of 10 1-cm segments							
1	2.3	2.3	2.8	2.8	2.8	3.0	2.2	2.60 ± 0.30[a]
2	1.0	0.8	1.3	1.0	1.2	1.4	0.8	1.07 ± 0.22
3	2.5	1.5	3.2	2.8	2.3	2.3	2.5	2.44 ± 0.48
4	1.8	1.8	2.7	1.5	1.2	1.4	1.7	1.73 ± 0.44
5	0.8	1.8	2.7	0.7	0.7	0.8	1.0	1.21 ± 0.70
6	0.8	1.5	1.7	0.7	0.7	0.8	1.0	1.03 ± 0.38
7	0.7	1.0	1.7	0.7		0.8	0.8	0.95 ± 0.40
8	0.7	1.0	1.3	0.5		0.8	0.8	0.85 ± 0.29
Hour	$LaCl_3$ (10 mM) at hour 1, N = 6							$\bar{X}$
	mm/h·column of 10 1-cm segments							
1	2.3	2.2	1.7	2.5	2.8	1.0		2.08 ± 0.67[a]
2	0.5	0.5	0.5	1.0	0.3	0.3		0.52 ± 0.27
3	1.2	0.8	1.2	0.5	0.8	0.8		0.88 ± 0.28
4	2.2	0.8	1.7	1.5	1.7	1.5		1.57 ± 0.48
5	2.5	1.5	2.8	2.2	2.8	1.5		2.22 ± 0.63
6	2.2	2.3	2.8	2.5	2.8	1.5		2.35 ± 0.51
7	2.2	2.3	2.7	2.5	2.0	1.5		2.20 ± 0.44
8	1.3	1.7		1.7	2.0	1.0		1.54 ± 0.48

[a] Confidence limits at the 95% level.

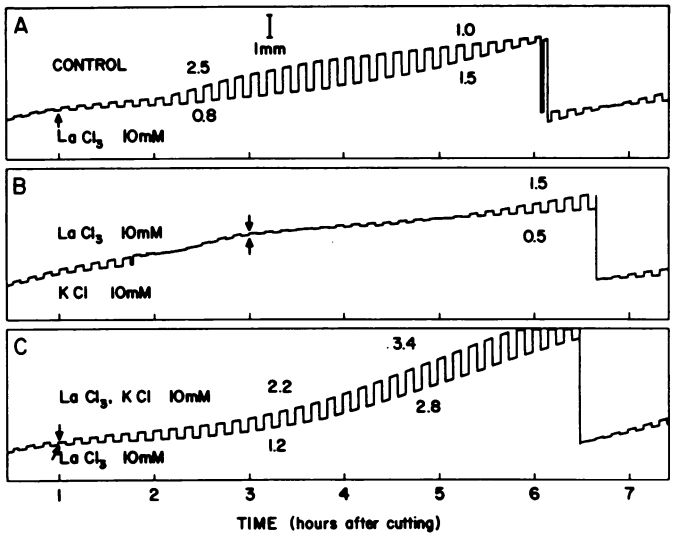

FIG. 1. Coleoptile elongation responses to $LaCl_3$ and KCl. A: response to 10 mM $LaCl_3$ administered at h 1 compared with control. B: response to 10 mM $LaCl_3$ compared with response to 10 mM KCl, treatments administered at h 3. C: response to $LaCl_3$ and KCl each at 10 mM compared with response to 10 mM $LaCl_3$, treatments administered at h 1. Values shown along the recording traces are rates expressed as mm/h·column of 10 1-cm segments.

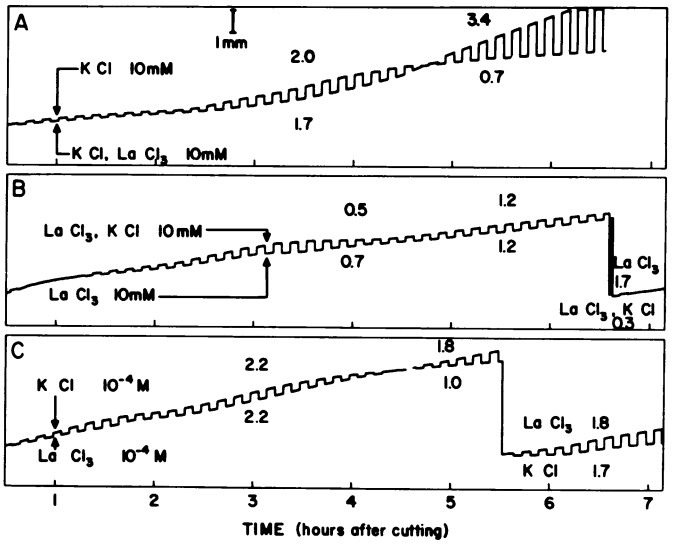

FIG. 2. Coleoptile elongation responses to $LaCl_3$ and KCl. A: response to 10 mM KCl compared with response to KCl and $LaCl_3$ each at 10 mM, treatments administered at h 1. B: response to $LaCl_3$ and KCl each at 10 mM concentration compared with response to 10 mM $LaCl_3$, treatments administered at h 3. C: response to 10^{-4} M KCl compared with response to 10^{-4} M $LaCl_3$, treatments administered at h 1. Values shown along recording traces are rates expressed as mm/h·column of 10 1-cm segments.

Application of the treatments at h 3 produced the results shown in Figure 2B. Both treatments slowed the SGR rate and produced the same rate of elongation over h 4 through 6. During h 7 (shown only by the values at the end of the recording) the elongation rate of the column of coleoptile segments in the $LaCl_3$ treatment increased while the combination treatment continued to elongate at a very slow rate. The difference between the mean lengths of the columns was 6.5 mm at h 20.

In Figure 2C a comparison of the effects of less concentrated KCl and $LaCl_3$ solutions on elongation rate is shown. At 0.1 mM, $LaCl_3$ administered at h 1 had no obvious effect on the onset of the SGR or its initial rate. During the 3rd h the elongation rate of the KCl treatment decreased while that of the $LaCl_3$ treatment increased. Measurements at h 20 were: $LaCl_3$ 64 mm, KCl 60 mm.

In Figure 3, A and B, a comparison can be made between the responses to NH_4Cl and $LaCl_3$ at 1 and 10 mM concentrations supplied at h 1. The effect of each of the ammonium treatments was immediate at both concentrations. The stimulation of elongation by NH_4Cl at 1 mM concentration was initially at a rate similar to that noted for the SGR of oat coleoptiles (Fig. 1A). A second increase in elongation rate occurred at the time of the SGR. This rapid rate of elongation persisted for 3 h. Ten mM NH_4Cl produced a rate of elongation comparable to that produced in response to IAA at 20 μM concentration. This rapid rate of elongation fell off rapidly and was spent in 2 h.

One mM $LaCl_3$ produced less delay of the SGR than did the 10 mM concentration. The late and prolonged stimulation of elongation by La^{3+} was much greater at the higher concentration.

Figure 3C shows the rapid growth responses to 10 mM concentrations of $LaCl_3$ and $CaCl_2$, respectively. The effect of $LaCl_3$ at this concentration was again (Fig. 1, A and C, Fig. 2A) a delay in the time of expression of the SGR and an extended duration of the SGR rate of elongation. The $CaCl_2$ treatment at 10 mM concentrations showed no SGR and continued elongating at a slow but very steady rate of 0.2 mm/h·column of 10 1-cm segments.

In Figure 4A it is shown that $LaCl_3$ at 5 mM concentration delayed the SGR about 1 h. At this concentration the inflection point is not clear because there was little inhibition of the initial rate of elongation and a gradual weak promotion of the SGR. It is clear from the recording that 5 mM $LaCl_3$ produced a growth response trace very similar to that obtained at 10 mM $LaCl_3$ (Fig. 3C).

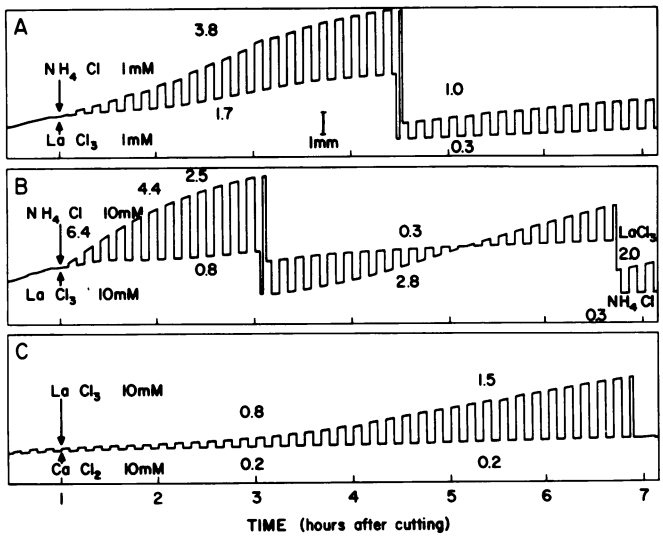

FIG. 3. Coleoptile elongation responses to treatments administered at h 1. A: response to 1 mM NH_4Cl compared with response to 1 mM $LaCl_3$. B: response to 10 mM NH_4Cl compared with response to 10 mM $LaCl_3$. C: response to 10 mM $LaCl_3$ compared with response to 10 mM $CaCl_2$. Values shown along recording traces are rates expressed as mm/h·column of 10 1-cm segments.

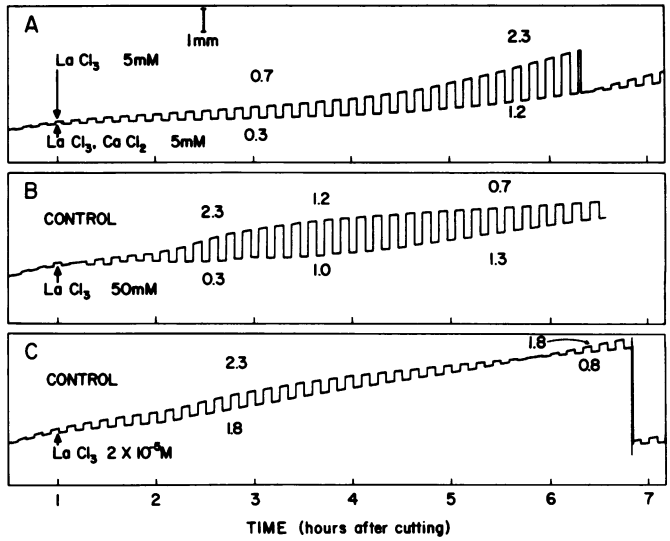

FIG. 4. Coleoptile elongation responses to treatments administered at h 1. A: response to 5 mM $LaCl_3$ compared with response to $LaCl_3$ and $CaCl_2$ each at 5 mM concentration. B: response to 50 mM $LaCl_3$ compared with control. C: response to 20 μM $LaCl_3$ compared with control. Values shown along recording traces are rates expressed as mm/h·column of 10 1-cm segments.

In comparison, the recording of the $CaCl_2$ and $LaCl_3$ treatment (Fig. 4A) shows that in combination the stimulation of elongation by $LaCl_3$ is delayed and reduced by the presence of $CaCl_2$.

Figure 4, B and C, shows the responses to a high and to a low concentration of $LaCl_3$. At 50 mM $LaCl_3$ the inhibition of elongation was immediate and similar to that noted for 10 mM $CaCl_2$ (Fig. 3C). The stimulatory effect was delayed about 2 h from the time of the control SGR. In the hormonal range of concentration of 20 μM $LaCl_3$, the recorder trace (Fig. 4C) shows an immediate inhibitory effect which lasts for about 1 h. Then a low but persistent rate of elongation permits the $LaCl_3$-treated column of segments to reach a greater length than the control by the end of the experiment.

Table I shows the rates of elongation hour by hour for both the controls (coleoptiles in 2% sucrose and 2.5 mM maleic acid buffer [pH 6.0]) and the 10 mM $LaCl_3$ treatments supplied at h 1. The course of elongation shown in numbers here presents a description of the elongation process very similar to that seen in Figure 1A and Figure 4, B and C. During the first 0.5 h in the rapid growth response recording apparatus there is an accelerated rate of elongation. At h 1 a slowing of the rate begins which reaches a very steady pace which persists until the beginning of the SGR at approximately 2.25 h from the time of cutting. This accelerated rate of elongation continues for about 1 h and then gradually tapers off to a rate of less than 1 mm/h·column of 10 1-cm segments during h 7 and 8.

Also shown in Table I is the effect on coleoptile elongation rate of 10 mM $LaCl_3$ in sucrose and buffer administered at h 1. The course of elongation shown in numbers here is very similar to that shown in Figure 1, A and C, for this treatment. The application of $LaCl_3$ has the effect of initially slowing the elongation rate. What appears to be a delayed SGR begins toward the end of the 3rd h. The accelerated rate of elongation does not develop as rapidly as the SGR of the controls nor does it attain the same magnitude. During h 3 the mean elongation rate for the $LaCl_3$ treatment (0.88 ± 0.28) is significantly different from that of the control (2.44 ± 0.48). The stimulation of elongation rate by $LaCl_3$ was found to reach its maximum during h 6, whereas the SGR response was found to reach its maximum during h 3. The

persistence of the $LaCl_3$-stimulated elongation rate is the noteworthy feature and is responsible for the greater final lengths of these columns of coleoptiles as compared with the controls. During h 7 the mean elongation rate of the $LaCl_3$-treated columns of coleoptiles is over twice that of the controls. The differences between the means of the control and the $LaCl_3$ treatment for h 3 and for h 6 are statistically highly significant.

It is appropriate to consider the difference between the inhibiting effect of $LaCl_3$ on coleoptile elongation in the *Avena* straight growth tests reported by Pickard (18) and the results reported here. The difference lies in the fact that in Pickard's experiments the coleoptile segments were placed immediately into the test solutions containing both IAA and La. Her results as stated represent the effect of La on the auxin stimulation of coleoptile elongation. Using the *Avena* straight growth test of 22 h, similar values were found in my laboratory. With the initial length of 9.3 mm using the same buffer and sucrose solution as used in the rapid growth response experiments, the following values for coleoptile elongation were determined: control, 12.5 ± 0.19 mm; IAA at 2 μM, 16.5 + 0.10 mm; IAA 2 μM with $LaCl_3$ at 10 mM, 13 ± 0.25 mm. These values are in good agreement with Pickard's data for a 24-h test: control, 14.1 mm; IAA at 20 μM, 21 mm; and IAA at 20 μM with 10 mM $LaCl_3$, 12 mm. The rapid growth response measurements depict the effect of La^{3+} and other cations on the endogenous growth rate of coleoptile segments and therefore do not conflict with the results of Pickard.

DISCUSSION

It has long been known that K^+ and Ca^{2+} have stimulatory and inhibitory effects respectively on auxin-stimulated growth in the *Avena* straight growth test (3, 23). More recently, the effects of these ions on the electropotential of *Avena* coleoptile cells have been measured. The transmembrane electropotential differences were increased from approximately 100 to 140 mv by Ca^{2+} and decreased to approximately 80 mv by K^+. It was the conclusion of Higinbotham *et al.* (11) that the increase in transmembrane electropotential gradient caused by external Ca^{2+} would tend to drive cations into the cell.

La^{3+} has been shown to affect coleoptile elongation in a much different way than does the Ca^{2+}, this being an initial inhibition of elongation followed by a prolonged stimulation of elongation by La^{3+} in contrast to continued inhibition of elongation by Ca^{2+}. Several bases for a differential in the effect of Ca^{2+} and La^{3+} upon membrane phenomena have been offered (1). La appears to bind irreversibly to the outer surface of the plasmalemma and competes with Ca for the binding sites which are involved in regulating monovalent cation transport.

Poovaiah and Leopold (19, 20) have investigated the effects of inorganic salts on tissue permeability and on the binding of auxin to membrane fractions and have suggested the stabilization and destabilization of macromolecules as a possible basis for the effects observed. Their suggestion was based on the work of von Hippel and Wong (25) in which the structure-making and structure-breaking effects were observed in purified proteins and DNA in neutral salt solutions of concentrations from 0.1 to 4 M. The interactions of externally supplied ions with the SGR suggest a complexity of ion effects beyond changes in the solubility of proteins in the order of the Hofmeister series. The effects of cations on membranes might better be related to interactions which can be observed at physiological salt concentrations. The salt concentration required to alter the stability of anionic lipid-protein complexes cited by Jones (13) is about 0.5 mM. The solubilization of an anionic lipid-protein complex is prevented by 0.5 mM Ca^{2+}. The alternative situation of enhancement of the permeability of membranes and a decrease in auxin binding to membrane preparations found in the presence of the ammonium ion indicates that the stability of the anionic lipid-protein complex is decreased. The effect of increasing the NH_4^+ concentration around coleoptile cells is the lowering of the cell electropotential difference (11).

La in producing a delayed but prolonged stimulation of the elongation rate is acting in a manner quite different from Ca. Although it has been suggested by Leonard *et al.* (14) that in corn roots La^{3+} inhibits K^+ absorption only over short influx periods, they also stated that Ca^{2+} has a similar effect. The similarity of the time course of K^+ influx (as $^{86}Rb^+$) for corn roots treated with 50 μM Ca^{2+} or La^{3+} led them to suggest that both influence K^+ influx without entering the cells. In addition it was noted that La^{3+} and Ca^{2+} stimulated K^+ absorption after 1 h.

These observations suggest that the cations La^{3+}, Ca^{2+}, K^+, and NH_4^+ are influencing the $H^+ - K^+$ antiport responsible for the acidification of the cell wall (2). The mechanism of this influence is postulated to be a modification of the stability of an anionic lipid-protein complex in the plasmalemma which may also be the binding site of auxin. This idea finds support in the reversible antagonistic effects of Ca and IAA on soybean plasmalemma membrane conformation demonstrated by Morré and Bracker (17) as well as in the reports on the chemical nature of the plasmalemma auxin-binding site by Ray *et al.* (21) and Cross and Briggs (4) which suggest that the binding site may be protected by membrane lipids.

The effects of La^{3+} on the endogenous elongation rate of coleoptile segments seem to provide a means to probe the relationship between membrane properties and cell growth.

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