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Osmoregulation in the *Avena* Coleoptile in Relation to Auxin and Growth[1]

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ABSTRACT

A study has been made of the effects of auxin and growth on the ability of *Avena* coleoptile sections to osmoregulate, *i.e.* to take up solutes so as to maintain their osmotic concentration, turgor pressure, and growth rate. The high auxin-induced growth rate of *Avena* coleoptiles is maintained when cells are provided sucrose, glucose, NaCl, or KCl as a source of absorbable solutes, but not when 2-deoxy-D-glucose or 3-*O*-methyl-D-glucose is used. In the absence of auxin, cells take up solutes from a 2% sucrose solution and the osmotic concentration increases. The rate of solute uptake is even greater in the presence of auxin or fusicoccin, but the osmotic concentration rises only slightly because of the water taken up during growth. Solute uptake is not stimulated by auxin when growth is inhibited osmotically or by calcium ions. Solute uptake appears to have two components: a basal rate, independent of auxin or growth, and an additional uptake which is proportional to growth. Osmoregulation of sections may be limited by the rate of entry of solutes into the tissue rather than by their rate of uptake into the cells.

The rate of plant cell elongation is sensitive to small changes in turgor pressure (5, 6). The uptake of water during growth will dilute the existing OS[3] and thus reduce the turgor pressure and the growth rate unless osmoregulation occurs; *i.e.* unless new solutes are produced or taken up into the cell so as to maintain the OC. The importance of osmoregulation to growth has been demonstrated with *Avena* coleoptiles in the following way (24). In the absence of exogenous solutes, auxin induces a rapid initial growth rate, but after 4 to 6 h the rate begins to decrease as the OC falls, and by 12 h the growth has nearly ceased. In contrast, the auxin-induced growth rate and the OC are maintained at a constant level for over 20 h if 2% sucrose is included in the medium. The importance of osmoregulation in maintaining rapid cell enlargement has also been demonstrated for stem (21, 22) and leaf tissues (9, 10).

The control of osmoregulation has been extensively studied in algae (16, 18), where a change in OC can be regulated by cell volume (17) or turgor pressure (12, 33), but little is known about its control in higher plants. The fact that auxin stimulates both sugar (1) and salt uptake (15) in *Avena* coleoptiles suggests that the osmoregulation could be under hormonal control. Alternatively, the increased osmoregulation could be in response to changes in cell volume or turgor. This study was undertaken to examine the control of osmoregulation in *Avena* coleoptile sections.

MATERIALS AND METHODS

Plant Material. Coleoptile sections were obtained as follows. Seeds of Avena *sativa* var. Victory were soaked in tap water for about 1 h, planted in vermiculite saturated with tap water, and the trays were covered and placed in a room lit with a dim red light at 26 C. Four-day-old seedings, whose coleoptile measured 25 to 35 mm, were harvested, the coleoptiles were deleafed, and a section of either 5 or 15 mm was cut from each coleoptile starting 3 mm back from the tip. The sections were immediately placed in distilled H_2O and preincubated on a shaker for a period of between 0.5 and 1 h to remove endogenous auxin and to randomize the sections. All of these manipulations were carried out under room lights and at room temperature.

OC Determinations. The OC was determined by two osmometric techniques. For freezing-point osmometry, forty-five 15-mm sections were removed from solution at the times indicated, their lengths were measured, and then they were blown and blotted dry, wrapped in aluminum foil, and placed on Dry Ice. At the end of the experiment, the foil packets were removed one at a time and thawed, after which the coleoptiles were placed between two glass slides and the cell sap was squeezed out into a vial. The OC was then measured directly with an Advanced Model 3L freezing point osmometer. Because 0.2-ml samples were required, which necessitated using large amounts of material, duplicates were not run. For vapor pressure osmometry, nine to fifteen 5-mm sections were removed, measured, dried, wrapped in lots of three, and frozen and thawed as above. Thawed sections were placed on a small filter paper disc and crushed with a spatula. The wet disc was then quickly placed in a Wescor Model 5100B vapor pressure osmometer and the OC was determined. For each time point there were three to five replicates. Vapor pressure osmometry is the method of choice since it uses fewer sections and it permitted us to employ the more homogeneous 5-mm sections rather than the 15-mm ones. The apparent OC values obtained by either of these methods may be lower than the actual OC values because of the presence of apoplastic solution. No correction has been made for this error, which in other systems is about 10% (3, 31), because we assume that the error would be a constant for all our OC measurements.

The osmotic concentration was also determined plasmometrically by a procedure modified from Bernstein and Nieman (2). Five 5-mm sections, either intact or with the cuticle and epidermis removed (7), were placed in each of 10 mannitol solutions ranging in concentration from 0 to 0.6 molal. A fixed amount of [^{14}C]-mannitol was also added to each solution as a tracer. The sections were incubated on a shaker for 4 h at 0 C, removed, blown, and blotted dry, and finally placed in 10 ml of Aquasol. The vials with the scintillant and sections were placed on a shaker at high speed

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[3] Abbreviations: OS, osmotic solutes, ΔOS, change in osmotic solutes; OC, osmotic concentration; FC, fusicoccin.

for 24 h and then counted on a Packard model 3320 liquid scintillation counter. Because mannitol is an impermeant solute over this time period, the number of counts in the tissue is proportional to the amount of free space present. At the point of incipient plasmolysis, the volume of free space begins to increase rapidly. The point of incipient plasmolysis is roughly equivalent to the internal osmotic concentration. Therefore, a plot of external mannitol concentration *versus* cpm will, in theory, yield a curve with a sharp break at the internal OC.

Growth measurements. Section length was measured with a dissecting scope fitted with a stage micrometer. Ten 5-mm sections were used per treatment for growth experiments and the average length determined immediately before (L_i) and at various times during the incubation period (L_f). Change in length (ΔL), expressed as a percentage, was calculated as

$$\Delta L = 100\,(L_f - L_i)/L_i.$$

Incubations. Incubations were carried out in 10 ml of a Tris-Mes buffer, made up to 10 mM in Mes and titrated with solid Tris to pH 6.0, and then diluted to 1 mM. IAA (titrated to pH 6 with KOH), sugars, KCl, and NaCl were added at the concentrations indicated for particular experiments. PEG 4000 was prepared so that the OC of the solution, containing PEG, 2% (w/v) sucrose and 1 mM Mes-Tris buffer was 0.22 Osm/kg. After incubation with PEG the sections were soaked in distilled H_2O for 20 to 30 min at 0 C prior to the final length measurement and subsequent OC measurement.

Calculation of OS. The OC and the section lengths were measured both before and after the incubation period. Since the amount of solutes (OS) is equal to the OC × cytoplasmic volume (V), and since for *Avena* coleoptiles V is proportional to the section length (26), the per cent increase in solutes (ΔOS) can be calculated by the equation:

$$\Delta OS = 100(OS_f - OS_i)/OS_i = 100(L_f \cdot OC_f - L_i \cdot OC_i)/(L_i \cdot OC_i)$$

where the subscripts *f* and *i* refer to final and initial measurements, respectively.

RESULTS

Osmotic Concentration of *Avena* Coleoptile Sections. Previous determinations of the OC of the *Avena* coleoptile by plasmolysis (5, 6, 24, 26) and freezing point osmometry of expressed sap (27) have given values from 0.38 to 0.45 osm/kg. However, we obtained OC values of 0.26 ± 0.012 (n = 18) by freezing point and 0.25 ± 0.015 (n = 49) by vapor pressure osmometry. Since these values are so much lower than those previously reported, they were checked by two plasmometric methods. The first involved incubating sections in various concentrations of mannitol, each with a trace amount of [^{14}C]mannitol. A plot of cpm *versus* external OC would be expected to yield a curve with a sharp break, which occurs at the internal OC (Fig. 1). The OC values of 0.28 ± 0.05 osm/kg (n = 6) obtained by this method confirms the validity of the osmometry values. In addition, visual observation showed that sections incubated in 0.2 M mannitol were not plasmolyzed while those in 0.3 M mannitol had a significant number of plasmolyzed cells.

Ability of External Solutes to Support Auxin-induced Growth. Auxin-induced coleoptile growth is stimulated over a 24-h period by exogenous solutes such as sucrose, glucose, NaCl, and KCl (23, 24, 28, 30). In the case of sucrose the initial high growth rate, instead of decreasing after 4 to 6 h, is maintained for at least 20 h (24) (Fig 2).

Glucose and sucrose (50 mM) are equally effective in maintaining a fairly constant growth rate of 5-mm sections for over 23 h. On the other hand, the glucose analogs, 2-deoxy-D-glucose and 3-*O*-methyl-D-glucose, which are frequently used to study glucose uptake (13, 14) inhibited growth. When the concentration of deoxyglucose was reduced to 5 mM, inhibition still occurred (data not shown), indicating that the inhibition was not osmotic, while the inhibition caused by methylglucose could be osmotic, since at 5 mM, the growth curve was indistinguishable from that of the

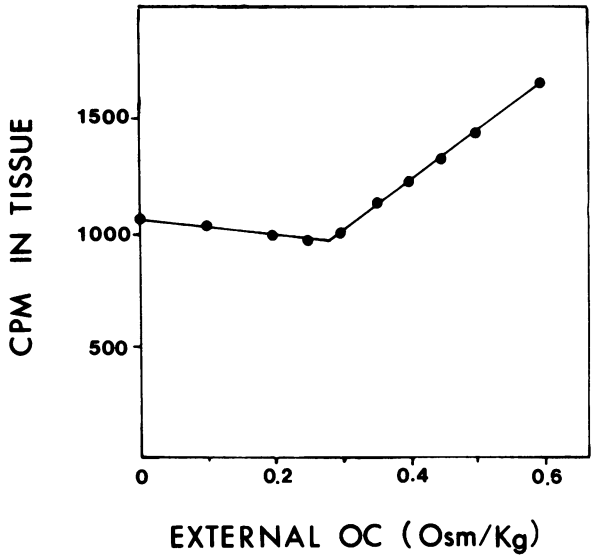

FIG. 1. Determination of OC of *Avena* coleoptile sections by the mannitol infiltration technique. Five 5-mm sections were incubated for 4 h at 0 C in 2 ml of 0 to 0.6 molal mannitol containing 0.5 μCi [^{14}C]mannitol and were then counted. The break in the curve occurs at the OC of the cells.

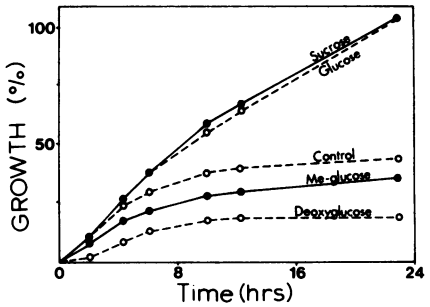

FIG. 2. Effect of exogenous sugars on the auxin-induced growth response of *Avena* coleoptile sections. Groups of ten 5-mm sections were incubated in 1 mM Mes-Tris buffer, pH 6.0 + 10 μM IAA and with 50 mM sugars as indicated.

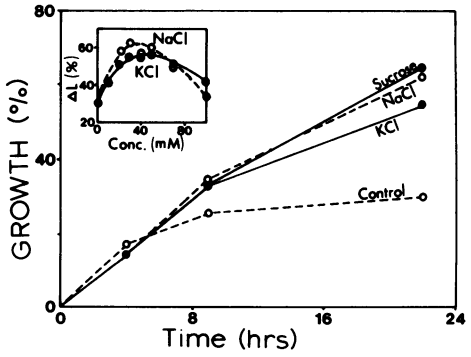

FIG. 3. Effect of KCl and NaCl on the auxin-induced growth response. Conditions were the same as in Figure 2 except 30 mM NaCl or KCl was used instead of sugars. Insert: Effect of varying concentrations of NaCl and KCl on growth over 22 h.

Table I. *Loss of Solute During Growth in the Absence of Any Absorbable Solute*

Sections were incubated 10 h in buffer ± IAA. OC was determined by vapor pressure osmometry. ΔOS was calculated as described under "Materials and Methods."

IAA	ΔL	OC	ΔOS
	%	*Osm/kg*	%
Initial		0.255	
+	38	0.167	−10
−	6	0.217	−10

Table II. *Effect of Auxin and FC on Uptake of Solute from 2% Sucrose Solution*

Sections were incubated 6 h in buffer and 2% sucrose, with or without 10 μM IAA or FC. OC was determined by vapor pressure osmometry.

Hormone	ΔL	OC	ΔOS
	%	*Osm/kg*	%
Initial		0.266	
IAA	30	0.319	+56
FC	21	0.310	+41
None	4	0.339	+32

Table III. *Ability of Sugars and Salts to Be Absorbed During Osmoregulation*

Sections were incubated 10 h in buffer + 50 mM sugars or 30 mM NaCl ± 10 μM IAA. Growth was measured and OC was determined by vapor pressure osmometry in Experiments 1 and 2, and by freezing-point osmometry in Experiment 3.

Expt.	Solute	IAA	ΔL	OC	ΔOS
			%	*Osm/kg*	%
1	Initial			0.249	
	Sucrose	+	55	0.270	+68
	Sucrose	−	8	0.323	+41
	Glucose	+	46	0.220	+28
	Glucose	−	8	0.278	+21
	Deoxyglucose	+	17	0.224	+5
2	Initial			0.254	
	Glucose	+	39	0.215	+18
	3-Methylglucose	+	24	0.212	+2
3	Initial			0.263	
	Sucrose	+	42	0.270	+45
	Sucrose	−	6	0.322	+29
	NaCl	+	37	0.259	+35
	NaCl	−	6	0.312	+26

control.

Both NaCl and KCl also supported continued growth (Fig. 3). The optimal concentration for both was between 30 and 50 mM (insert, Fig. 3), but Na^+ supported slightly more rapid elongation than did K^+. This may seem surprising since *Avena* coleoptile plasma membranes have been shown to import K^+ and export Na^+ actively (25), but similar results have been obtained with *Avena* coleoptiles (24) and barley coleoptiles (23). In some experiments, 30 mM NaCl decreased the growth rate duing the first 4 h compared with the controls, probably due to an osmotic reduction in turgor. A similar effect was often seen with KCl or sucrose, as well. Thereafter, the growth rate remained high in the presence of NaCl while it fell in the absence of absorbable solutes.

The Control of Osmoregulation. We have examined the effects of auxin and absorbable solutes on osmoregulation. Since the maintenance of turgor is of interest here, the OC was chosen as the most applicable measurement rather than influx rates. From OC and length measurements we then calculated the net increase in solute content (ΔOS) of the tissue. No attempt was made to determine the chemical nature of the solutes.

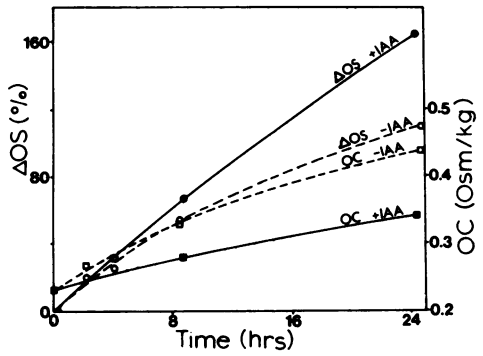

FIG. 4. Changes in the OC and ΔOS of sections during a 24-h incubation in buffered 2% sucrose ± 10 μM IAA. Note that the auxin-treated sections have a greater ΔOS than the minus-auxin controls, but have a lower OC due to dilution of the cell contents by water during growth.

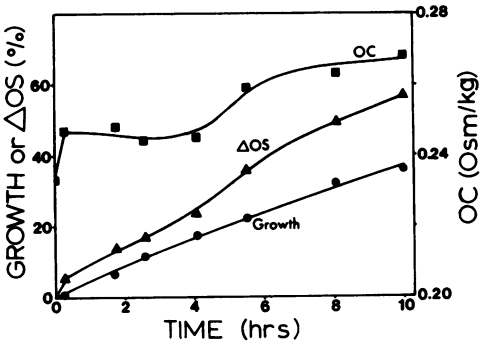

FIG. 5. Changes in OC and ΔOS of auxin-treated sections over short time periods. Groups of 15-mm sections were pretreated 30 to 60 min in water, then transferred to 1 mM Mes-Tris buffer, pH 6.0, containing 2% sucrose and 10 μM IAA. OC was determined by freezing-point osmometry. The initial rise in OC is probably caused by the transfer of sections from water to the sucrose solution and not a response to auxin.

In the absence of external solutes (Table I), OC decreased markedly, especially in the auxin-treated tissues. This would be expected of cells taking up large quantities of water. But in addition, the total amount of solute in the tissue decreased, and the decrease was independent of auxin. This decrease in solute could occur through polymer synthesis, metabolism, or leakage of internal solute.

In the presence of sucrose and IAA, there is a large gain in solutes and a small increase in OC (Table II). There is an even larger increase in OC in the absence of auxin, but the ΔOS is less than in the presence of auxin. Similar results were seen when FC was used in place of IAA (Table II), although the FC stimulation of ΔOS is not as pronounced as that seen with IAA. Sucrose is not the only solute to permit osmoregulation to occur. For example, OC is maintained in the presence of glucose (Table III) and the ΔOS is enhanced by auxin. With glucose the ΔOS is only about half what it is with sucrose under identical conditions. The glucose analogs, 2-deoxy-D-glucose and 3-*O*-methyl-D-glucose not only fail to support continued auxin-induced growth, but are not readily absorbed by *Avena* coleoptile cells. For example, 2-deoxy-D-glucose caused only a 5% ΔOS, as compared with a 28% ΔOS for glucose. Likewise, 3-*O*-methyl-D-glucose gave only a 2% ΔOS as compared with an 18% ΔOS for glucose in a different experiment. On the other hand, NaCl, which supports continued growth, causes a large increase in ΔOS (Table III) and IAA enhances this osmoregulation. Again, the ΔOS is not as great with NaCl as it is with sucrose.

Table IV. *Lack of Effect of Auxin on Solute Uptake When Growth is Inhibited*

Sections incubated 10 h in buffer + 2% sucrose ± IAA and with addition of PEG 4000 (OC_s = 0.220 osm/kg) or 50 mM $CaCl_2$. Growth measured and OC determined by vapor pressure osmometry.

Inhibitor	IAA	ΔL	OC	ΔOS
		%	*Osm/kg*	%
Initial			0.276	
None	+	56	0.260	+47
None	−	6	0.314	+21
PEG	+	7	0.320	+24
PEG	−	1	0.327	+20
Initial			0.261	
None	+	45	0.280	+56
None	−	6	0.339	+38
$CaCl_2$	+	3	0.340	+34
$CaCl_2$	−	2	0.356	+39

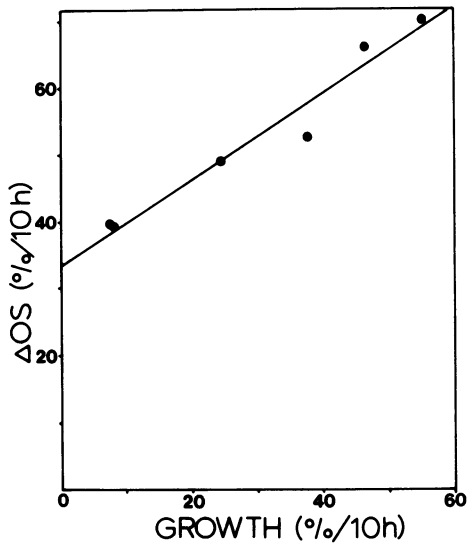

FIG. 6. Relation between the rate of osmoregulation and the growth rate. Groups of 5-mm sections were incubated for 10 h in buffered 2% sucrose, with 0, 0.01, 0.1, 0.3, 1, or 10 μM IAA. Growth was measured, OC was determined by vapor pressure osmometry, and ΔOS was calculated.

The kinetics of sucrose uptake have been examined in some detail. Figure 4 shows that in the absence of auxin OC rises steadily and no plateau is reached within 24 h. In the presence of IAA, OC also increases, although at a much reduced rate compared with the minus auxin control. The ΔOS, on the other hand, increases more rapidly with auxin. The details of the changes in OC and OS in the first 10 h show that OC remains nearly constant for 4 to 7 h after addition of auxin, after which there is a slow rise in OC (Fig. 5). In some experiments (*e.g.* Fig. 5), there was an initial increase in OC, but this was apparently caused by the transfer of the sections from water to the auxin-containing 2% sucrose solution rather than to auxin itself since this rise never occurred when sections were preincubated in 2% sucrose (data not shown). Although the points in Figure 5 are not statistically different from each other, the pattern of a plateau and then a slow rise in OC was observed in each of five experiments.

The auxin-induced increase in ΔOS could be a direct response to auxin or it could be an indirect effect, related to the increased growth which occurs in the presence of auxin. To determine whether the IAA effect is a result of primary or secondary processes, growth was inhibited by two methods and the ability of auxin to enhance osmoregulation under these conditions was determined. Growth was first inhibited osmotically with PEG 4000 (Table IV). The external OC was sufficient to reduce turgor pressure such that very little growth occurred. PEG almost completely blocked the IAA stimulation of sucrose uptake; what little remained could be attributed to the incomplete inhibition of growth. PEC itself did not increase solute uptake, suggesting that low turgor pressure did not enhance sucrose uptake. Similar results were obtained when growth was inhibited osmotically with 0.25 M mannitol (data not shown). Growth was also inhibited with 50 μM $CaCl_2$ (Table IV). Again, no auxin-increased ΔOS was observed in the absence of growth. Thus, both techniques show that the increase in sucrose uptake is a secondary effect of IAA. Similar results have been shown for uptake of C^{14} glucose (1).

Finally, in order to examine the relationship between growth and solute uptake, the IAA concentration was varied between 0 and 10 μM and ΔOS was then plotted as a function of the growth rate (Fig. 6). The results suggest that two processes are involved in osmoregulation: there is a basal rate of solute uptake which is independent of growth, and a second component which is proportional to the growth rate.

DISCUSSION

The rate at which a cell elongates is controlled by four parameters; the hydraulic conductivity, wall extensibility, the wall yield stress, and the osmotic potential (20). When an agent such as auxin induces an increase in the growth rate there must be a change in one or more of these parameters. It has already been demonstrated that in *Avena* coleoptiles auxin causes an increase in wall extensibility while it does not alter the wall yield stress (8). The effect of auxin on the osmotic potential, and thus the turgor pressure, has been uncertain. Ordin *et al.* (24) reported that in the absence of exogenous solutes the OC actually decreased during auxin-induced coleoptile growth. We have confirmed these results (Table I). We conclude that auxin does not induce growth by causing an increase in OC. On the other hand, auxin is known to increase the uptake of glucose (1) and K^+ (15) into coleoptile tissues, and the fact that sucrose and NaCl both promote coleoptile growth (25, 30) suggests that auxin might enhance their uptake as well. This added solute uptake, while not sufficient to increase the OC during the initial period of growth, could be important in preventing a drop in turgor.

In this study we have measured OS rather than the flux of any one solute. It has been shown that the accumulation of solutes (osmoregulation) is greater in the presence of auxin (or FC). This increase is actually in response to auxin-induced growth rather than to auxin itself, as shown by the fact that when growth was inhibited osmotically or with calcium ions, the effect of auxin on osmoregulation was abolished (Table IV).

The osmoregulation which occurs during auxin-induced growth is important for growth as is indicated by the fact that the initial auxin-induced growth rate can be maintained for only a few h unless absorbable solutes are present in the external medium. However, the rate of growth is not correlated with the rate of osmoregulation. This is shown as follows: sections incubated with 50 mM sucrose or glucose grow at the same rate, yet the ΔOS of the sucrose-treated sections is twice that of the glucose-treated ones (presumedly because sucrose is cleaved into glucose and fructose) and the OC of the sucrose-treated ones is, as a consequence, also higher (Table III).

If osmoregulation is not directly regulated by hormones, how is it regulated in coleoptiles? In some algae, such as *Valonia ventricosa* (12, 33) solute uptake is controlled by the turgor pressure. When turgor decreases, solute uptake is increased, and vice versa. This does not appear to be the situation in *Avena* coleoptile sections. The presence of external osmotica such as mannitol or PEG failed to increase the ΔOS (Table IV). Likewise, solute uptake continued at a considerable rate even after a significant increase had occurred in the OC (Fig. 4). Although changes in

OC do not necessarily produce parallel changes in turgor pressure, these results are not consistent with a turgor-control of osmoregulation.

Osmoregulation is controlled in other algae by the volume or surface area of the cells (17). The relationship between the growth and the ΔOS shown in Figure 6 might seem to indicate that uptake is simply proportional to the surface area of coleoptile cells. In fact, this seems unlikely. Because the surface area is increasing constantly over a 24-h incubation with auxin, the rate of increase in OS should also increase continually. Instead, the rate of ΔOS remains constant over this period (Fig. 4).

A final possibility is that the rate of osmoregulation is determined by the rate of entry of solutes into the tissue rather than into the cells. Because the cuticle has a low permeability to sugars or cations (19), most solutes must enter the tissue through the cut ends. The limiting step in the osmoregulation of nongrowing tissues may be the rate of diffusion of solutes through the cut ends. As tissues grow, there would be bulk flow of water into the tissue which could bring additional solutes into the tissue. In this case the rate of ΔOS would be expected to be constant over time since it would be proportional to the growth rate which remains nearly constant. In order to determine the validity of this idea, osmoregulation must be examined in tissues in which the cuticle is removed as a barrier to solute uptake.

We were surprised to obtain in this study OC values of 0.24 to 0.28 osm/kg for freshly cut *Avena* coleoptile sections, since previous determinations had given values in the 0.35 to 0.45 osm/kg range (5, 6, 24, 26, 27). The reason for this large difference in OC is not known. Most of the previous determinations made use of a different method to measure OC, visual determination of incipient plasmolysis, but it seems unlikely that this could account for such different values. A more likely possibility is that the OC is dependent on the conditions used to grow the seedlings, such as the type of vermiculite used, the humidity, and lighting of the chamber, or the particular seed lot used. It is apparent that one should not rely on the OC values in the literature, but should determine it directly whenever the OC value is of importance. Our low OC values are not unreasonable, inasmuch as similar values have been recorded for a variety of other growing plant tissues, including coleoptiles of wheat (11), barley (23), and rice (32), and hypocotyls of lettuce (29), sunflower (21), and soybean (4).

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