showed reliable responses to rapid change in water conditions of plants. With proper calibrations, leaf water and internal water (relative turgidity or diffusion pressure deficit) changes can be followed.

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Uptake of Indole-3-acetic Acid and Indole-3-acetonitrile by Avena Coleoptile Sections [1, 2]

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Introduction

The rates of uptake of auxins as a factor controlling the growth response have so far received much less attention than their chemical structure. In particular, the activity of indole-3-acetonitrile (IAN) presents a special problem which focuses attention upon its rate of uptake into the tissue.

When IAN was isolated from crucifers by Jones et al. (7), and shown to possess auxin activity up to 10 times as great as that of IAA in the Avena coleoptile straight growth test, it was concluded (3) that the activity could not be due to its conversion to IAA. However, Thimann (12) showed that in the slit pea curvature test IAN has virtually no activity, yet it becomes effective in this test after having been in contact with slit Avena coleoptiles for 48 hours. Thus, Avena tissue so modified IAN as to make it active upon Pisum. It was deduced that the IAN was being converted to IAA by an enzyme present in Avena but not in Pisum. The conversion was confirmed chromatographically (11), and the enzyme, nitrilase, has subsequently been purified and characterized (14, 15).

If IAN is active on Avena only through its conversion to IAA, then the fact that it is more active (mole for mole) than IAA calls for a special explanation. It was suggested (e.g. 12) that the difference may be ascribed to a much more rapid uptake of IAN than of IAA. In other plants where the activity is real, but less than that of IAA (8), or not proportional to concentration at all (13), it has been suggested that activity is limited by the slow rate of

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conversion to IAA. Although in a few plants qualitative differences between the responses to IAA and to IAN have been reported (1, 5), there is no conclusive evidence as yet that IAN can show auxin activity without hydrolysis to IAA. A slight synergism between IAN and IAA has been claimed (9) but Bentley and Housley (3) found no evidence of synergism in Avena. The presence of IAA cannot invariably be detected in tissue which shows a growth response to IAN, but this would naturally depend on the relative rates of IAN hydrolysis and of the utilization and destruction of IAA.

The availability of C^{14}-labeled IAN and IAA enabled the uptake of the 2 auxins to be quantitatively compared in the present investigation. The prediction that IAN must enter the coleoptile sections more rapidly than IAA has been confirmed.

Materials and Methods

Svalöf Victory oats were soaked in water for about 4 hours and sown without dehusking in moist vermiculite to a depth of 1 cm. The seedlings were grown in a darkroom at 25° and 85% relative humidity, illuminated occasionally with dim red light. Red light treatment was given for 4 hours early on the third day, so as to inhibit the growth of the mesocotyls. On the fourth day, when the plants were about 100 hours old, coleoptiles between 2.5 and 3.0 cm long were selected, and a single 5 mm section was cut from each at a distance of 3 mm from the tip. The leaf was then pushed out with a thin glass rod. Ten of the sections were floated on 10 ml of distilled water for exactly 90 minutes, then transferred to 1 ml of C^{14}-auxin solution in a shell vial (2 cm diam). At the end of the uptake period, the sections were removed one by one, and held in specially adjusted forceps to allow a rapid rinse from a wash bottle of distilled water. (It was found that these sections showed the same activity as sections cut longitudinally and blotted to remove the auxin solution.) The 10 sections were dried for 15 minutes at about 80° on an aluminum planchet, ground in a little alcohol with a glass rod, and dried again. The radioactivity on the planchet was finally counted under a Geiger tube.

To measure uptake under nitrogen, the sections were transferred immediately after cutting to a Thunberg tube containing 1 ml of distilled water. After 60 minutes, the tube was evacuated and refilled 3 times with 100% oxygen-free nitrogen, and after a further 30 minutes, 1 ml of C^{14}-auxin solution of twice the desired concentration was added from the sidearm. In the same experiment, Thunberg tubes containing control sections were evacuated and refilled with air before the addition of the auxin. The sections were dried and counted in the usual manner.

One sample of C^{14}-IAA, labeled in the carboxyl group, was synthesized in the laboratory according to the method of Stowe (1963). A sample of higher activity, and a sample of cyanide-labeled IAN prepared by the same method were kindly supplied by Dr. Stowe. The 3 stocks used were: A) IAA, 5.4 μc/mg, or 2.10×10^9 dpm/mmole; B) IAA, 96.6 μc/mg, or 3.75×10^{10} dpm/mmole; C) IAN, 7.2 μc/mg, or 2.51×10^9 dpm/mmole.

All were dissolved in acetonitrile and kept at low temperature under nitrogen. Aqueous stock solutions were prepared by adding aliquots to distilled water and warming to drive off the acetonitrile. In the experiments of figure 2, 0.01 M potassium phosphate buffer, which has been shown on many occasions not to interfere with growth, was added. The purity of the IAA was checked by chromatography; a single spot containing about 96% of the radioactivity coincided with the R_F of authentic IAA.

The activities and concentrations of the aqueous stock solutions were determined by counting samples of 10 μl dried on aluminum planchets. It was found that when larger volumes of IAN solution were used, there was an appreciable loss of activity during drying. In order to insure that the 10 μl samples gave reliable results, and that there was no loss of activity from the sections during drying, the data for one complete experiment (fig 6) were obtained by scintillation counting. The proportion of each auxin absorbed by the tissue agreed closely with that calculated from other experiments.

The dry weight of 10 coleoptile sections, 5 mm long, was about 2 mg, and the fresh weight about 35 mg. The self-absorption correction for this amount of tissue was calculated by adding aliquots of the stock solution to the dried and ground tissue. The counts for the 3 solutions in presence of the coleoptile tissue were respectively 81%, 78%, and 79% of the counts in the absence of tissue. All counts of activity in coleoptiles have accordingly been corrected by a factor of 1.25. Corrections for background and counting efficiency (usually 33%) have been made, and the results are expressed in dpm per 10 (5 mm) coleoptile sections.

Results and Discussion

Time Course of Uptake. Figure 1 shows the increase in radioactivity of coleoptile sections floating

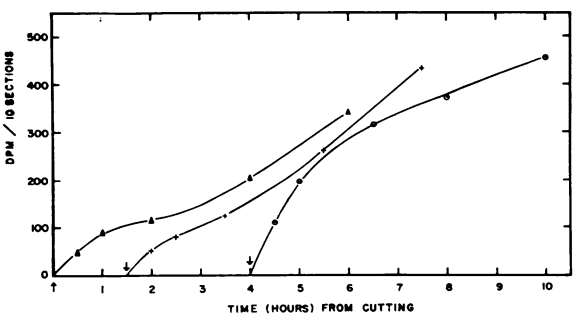


FIG. 1. Time course of increase in radioactivity in Avena coleoptile sections after transfer to C^{14}-IAA (7.5×10^{-8} M IAA, 2810 dpm/ml.) at various times after cutting. △, Transferred immediately after cutting. +, Transferred after 90 minutes on distilled water. O, Transferred after 4 hours on distilled water.

on unbuffered C^{14}-IAA solutions for periods up to 6 hours. Each point represents the activity in an independent sample of 10 sections, and the 3 curves show how uptake is affected by the time elapsing between cutting the sections and transferring them to the C^{14}-auxin solution. In sections transferred immediately after cutting, uptake is rapid for about the first hour, then slows down, and finally increases again. Sections transferred after 1.5 hours on distilled water behave similarly except that the lag is not so apparent. However, a slight lag occurring 90 to 180 minutes after the beginning of uptake has been observed consistently (fig 2). After 4 hours on water the initial uptake is still more rapid and extensive, and no lag appears, though the rate slows down after an hour or so. In a similar experiment using 0.02 M potassium phosphate, pH 4.5, the rate of uptake with time was about twice as great as from the unbuffered solution, but the same changes of rate were observed. These changes are therefore probably not due to the excretion of acid by the sections. Uptake of C^{14}-IAN also showed a similar pattern, which is apparently characteristic of uptake from very low concentrations of these auxins (figs 2, 4).

These time curves are similar to those observed by Andreae and Van Ysselstein (2) in pea epicotyls. Curves somewhat resembling those of figure 4 were found also with C^{14}-2, 4-D by Johnson and Bonner (6).

In all other experiments reported here the coleoptile sections were floated on distilled water (or buffer in the pH experiments) for 90 minutes after cutting, and then transferred to the C^{14}-auxin solution.

The Effect of pH. Figure 2, A and B, shows the incorporation of activity from dilute solutions of IAN and IAA at pH 4.5 and pH 7.5. In addition to the auxins, the solutions contained 0.01 M dipotassium phosphate adjusted to the required pH with phosphoric acid. The sections were floated on solutions of the same buffer during the 90 minute interval between cutting and transferring to the auxin solutions. The uptake of IAA at pH 4.5 is approximately 5 times that at pH 7.5, whereas the uptake of IAN shows no significant effect of pH. The concentration reached in the tissue in the IAN solution at 1 hour is about 2.5 times the external, while that in the IAA is somewhat below the external; thus about 3 times as much IAN is taken up as IAA, even at pH 4.5.

The same effect of pH on the uptake of IAA, but not on that of IAN, is shown in table II.

It will be noted from figure 4 that when concentrations higher than those in figure 1 were used the rates of uptake showed less fluctuation, but the initial rapid rise was still evident with both IAA and IAN.

The Relative Rates of IAN and IAA Uptake. Figure 3 summarizes all results relating to uptake from unbuffered solutions by sections transferred to auxin 90 minutes after cutting. The uptake of auxin is calculated as the concentration in the tissue, and both this and the concentration of the solution are plotted on a logarithmic scale. The 2 lines at left

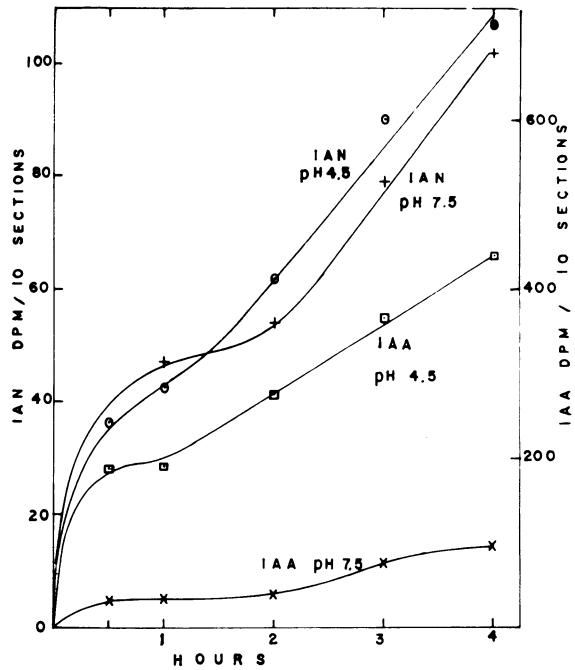


FIG. 2. The effect of pH on uptake from 2×10^{-7} M IAN, 508 dpm/ml, and 1.6×10^{-7} M IAA, 5890 dpm/ml, containing 0.01 M dipotassium phosphate, adjusted to pH 4.5 or pH 7.5 with phosphoric acid.

show the activity taken up in the first 30 minutes. At a concentration of 10^{-6} M, IAN uptake is four and a half times that of IAA. At 10^{-7} M, the ratio IAN uptake/IAA uptake approaches ten. The continuing uptake after the first hour is indicated at the right, where it can be seen that the IAN taken up from a concentration of 10^{-6} M is still about twice that of IAA at the same concentration.

The Effect of Concentration. The fact that the slopes in figure 3, especially those for the first to the fourth hour, are close to 45° means that uptake is nearly proportional to concentration over a wide range. It follows, then, that addition of unlabeled IAA to the solution should not appreciably affect the uptake of label, at least up to 5×10^{-4} M. However, a close study revealed that the situation is not quite so simple.

Figure 4 shows an experiment in which unlabeled IAA was added to the solution containing the isotope. The lower curve shows uptake from the C^{14}-IAA solution alone, diluted to 2.4×10^{-6}M. The upper curve shows the uptake when the same number of dpm are supplied with the addition of 20 times as much unlabeled IAA. It is evident that the addition of the unlabeled IAA actually increases somewhat the uptake of label. This ability of higher concentrations of auxin to cause somewhat more than proportional uptake was found in nearly all experiments with IAA, including those in which the solution was buffered at pH 4.5 or pH 7.5. Indeed, figure 3 shows slopes definitely a little greater than 45°, which is

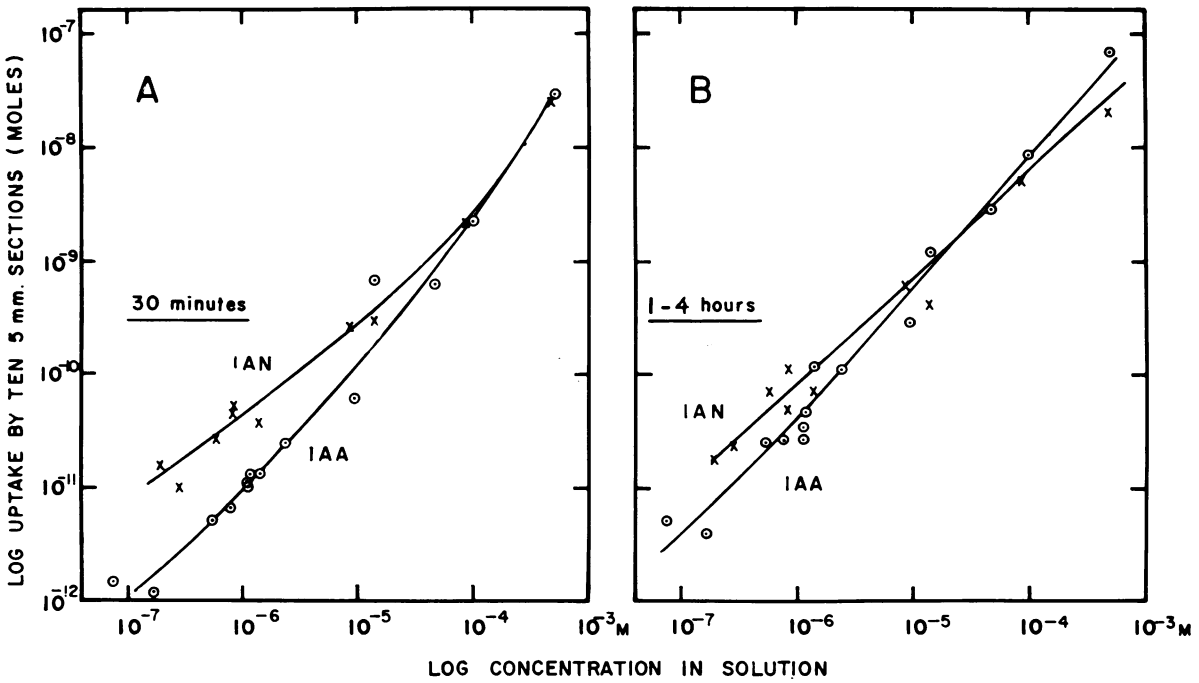


FIG. 3. The uptake of IAA and IAN in relation to external concentration. Each point represents a separate experiment. All solutions unbuffered. A, First 30 minutes of uptake. B, Steady-state uptake from the end of the first to the end of the fourth hour. ⊙, IAA. ×, IAN.

another way of saying the same thing. Thus, "IAA promotes the uptake of IAA."

Representative experiments on the uptake of C^{14}-IAN are also shown in figure 4. As compared with IAA it is seen that with IAN a somewhat higher proportion of the activity supplied enters the tissue. Thus, after 4 hours, the activity in 10 sections is 6.2% of that of the external IAA solution, but 12.2% of that of the IAN solution. The initial rapid phase of uptake is also more pronounced with IAN than with IAA. Increasing the concentration by the addition of unlabeled IAN tends to result in a more linear uptake curve, but there is no evidence here that IAN enhances its own uptake.

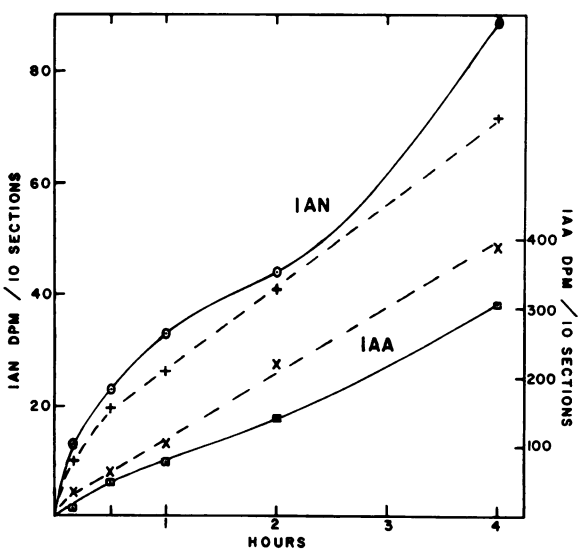


FIG. 4 Effect of unlabeled auxins on uptake of label. Solid lines, C^{14}-auxins alone. Broken lines, C^{14}-auxin with unlabeled auxin added. □, IAA, 5050 dpm/ml, 2.4×10^{-6} M. ×, IAA, 5050 dpm/ml, 4.7×10^{-6} M. ⊙, IAN, 720 dpm/ml, 3×10^{-7} M. +, IAN, 720 dpm/ml, 9×10^{-6} M.

Since the effects of concentration on the uptake of IAA and of IAN were consistently different, a further experiment was designed to study the effect of unlabeled IAA on the uptake of C^{14}-IAN, and of unlabeled IAN on the uptake of C^{14}-IAA. The results (table I) show that unlabeled IAA promotes the uptake of C^{14}-IAN, and unlabeled IAN promotes the uptake of C^{14}-IAA. However, (in agreement with fig 4) unlabeled IAN failed to promote the uptake of C^{14}-IAN. In the case of IAN, it seems possible that the stimulatory effect of higher concentrations may be present but be offset by competition for the hydrolyzing enzyme. If we bear in mind that the IAN has only 8% of the specific radioactivity of the IAA, table I also exemplifies the point made in figure 3A, namely that when the external concentration of auxin is very low, the uptake of IAN greatly exceeds that of IAA.

The promotion of auxin uptake by auxin itself is not a large effect but is not particularly easy to explain. It may result from the increased respiration rate induced by the auxin. Johnson and Bonner (6) observed no such effect with C^{14}-2, 4-dichloro-

Table I

Uptake of Radioactivity at 25° into 5 mm Avena Coleoptile Sections from 1 ml of 2×10^{-7} M C^{14}-IAN (508 dpm/ml) and of 1.7×10^{-7} M C^{14}-IAA (6330 dpm/ml)

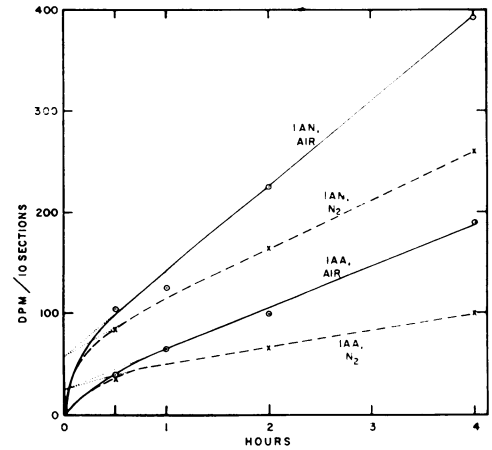
	dpm/10 sections	
	After 1 hr	After 3 hr
C^{14}-IAN alone	48	67
$+ 5 \times 10^{-4}$ M IAN	40	65
$+ 10^{-4}$ M IAA	76	113
C^{14}-IAA alone	66	120
$+ 5 \times 10^{-6}$ M IAN	121	245

phenoxyacetic acid, though they did note that the addition of unlabeled IAA did not decrease its uptake.

The data of figure 4 allow an estimate of the average concentration of auxin attained in the tissue. Since the volume of ten 5 mm coleoptile sections is about 0.035 ml, and the C^{14}-auxin is contained in 1 ml of solution, the average concentration of auxin in the tissue will equal that in the solution when 3.5% of the activity supplied is found in the tissue. This point is generally passed within an hour or 2, and the uptake shows no sign of slowing down within 4 hours. At this time the concentration reached in the tissue, as an average of 5 experiments, was found to be twice the external in IAA, but 5 times the external in IAN. It is worth noting that in some earlier (unpublished) experiments with potato tuber slices in naphthaleneacetic acid the concentration reached in the tissue was found to be 3 times the external. There can be doubt, therefore, that true accumulation of both IAA and IAN occurs in these tissues.

Physical and Metabolic Uptake. Figure 5 compares the uptake of both auxins in air with that in oxygen-free nitrogen. Uptake under nitrogen continues for at least 4 hours, although by this time the concentration of IAN in the tissue is more than 3 times that in the solution. Energy for the accumulation may thus be supplied by anaerobic reactions, even though to a lesser extent than by aerobic ones. However, extrapolation to zero time (dotted lines) shows that the initial rapid phase is not significantly decreased under nitrogen, whereas the subsequent rate of uptake is only about one half of that in air. Thus the initial uptake appears to be independent of aerobic metabolism.

When coleoptile sections are transferred to water or unlabeled auxin after a period in C^{14}-auxin, a proportion of the absorbed radioactivity is rapidly lost from the tissue. This gives an indication of the amount of auxin which has entered the tissue but which has not been accumulated within a permeability barrier or otherwise bound in the tissue. Figure 6 shows the activity remaining in the sections after varying periods of up to 4 hours in the auxins, followed by transference to water for 30 minutes thereafter. After the shortest period of uptake, 50% of the absorbed IAA or IAN was lost, whereas after longer periods of uptake, progressively smaller proportions of activity (and, indeed, smaller absolute amounts) could be removed in this way. Thus the



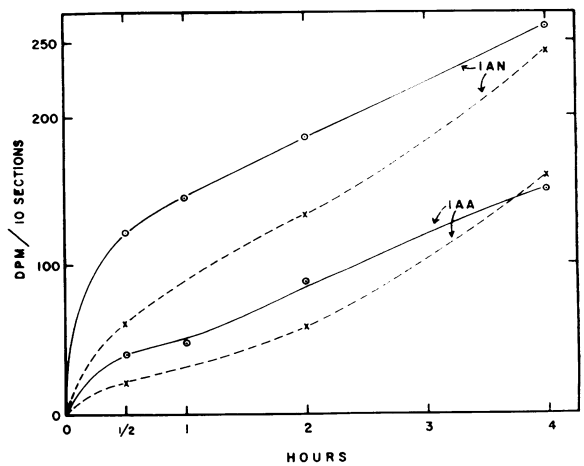


FIG. 5. (above). Effect of oxygen-free nitrogen on uptake from 8.6×10^{-7} M IAN, 2160 dpm/ml, or 1.1×10^{-6} M IAA, 4420 dpm/ml.

FIG. 6. (below). Loss of radioactivity on removal from C^{14}-auxin solutions. Solid lines, activity in sections after uptake period. Broken lines, activity remaining after 30 more minutes on water. Uptake from 8×10^{-7} M IAN, 2160 dpm/ml, or 1.1×10^{-6} M IAA, 4420 dpm/ml.

auxin in the physical phase is slowly entering beyond the permeability barrier.

Table II shows the results of another experiment, carried out at pH 4.5 and 7.5 (the 2 pH values used in figure 2), but counted only after 4 hours. At this time about 20% of the activity can still be lost from sections that have been in IAN, but not from those that have been in IAA. This is in agreement with the data at 4 hours shown in figure 6. The powerful effect of pH on IAA uptake compares well with that in figure 2.

Thus: A) much of the auxin taken up in the first 30 minutes can be readily lost again by diffusion; and B) its uptake is not dependent on oxidative processes. The subsequent, steady-state, uptake is decreased in nitrogen and may perhaps require only an excessively low concentration of O_2.

From the extrapolation to zero time in figure 5 it appears that of the IAN uptake measured at 30

Table II

Effect of Exposure of Sections to unlabeled IAN or IAA after Uptake from C^{14}-IAN (10,200 dpm/ml) or from C^{14}-IAA (13,000 dpm/ml) respectively

Uptake solution	pH	dpm/10 sections after 4 hr
IAN 4.1×10^{-6} M	4.5	1030
IAN 4.1×10^{-6} M	7.5	1100
IAA 6.2×10^{-6} M	4.5	1170
IAA 6.2×10^{-6} M	7.5	264

Second solution	dpm after a further 30 min in second solution (unlabeled auxin)	Decrease as % of original uptake
IAN 10^{-4} M	805	22
IAN 10^{-4} M	875	20
IAA 10^{-4} M	1240	...
IAA 10^{-4} M	260	2

minutes about 55% is due to the initial, rapid physical phase. Correspondingly from figure 6 the amount lost after 30 minutes on water was 55% of the amount taken up, with IAN, and 50% with IAA. The good agreement justifies the conclusion that it is the initial physical uptake of both substances which is reversible on transfer to water. In the case of IAN, however, this physical uptake corresponds to an apparent free space equal to 80% of the tissue volume. Thus the lipophilic nature of IAN must enable it to become concentrated either in the cell walls or in some more limited lipophilic phase of the tissue. If it is the latter, then those recorded instances where the effects of IAN are not identical with those of IAA might arise from a different distribution of these auxins within the cells or tissue.

In conclusion, it is clear that Avena coleoptile sections do take up IAN and IAA from solution at significantly different rates. If we compare these uptake rates with the relative growth activities of the 2 compounds (3, 12, 13) it appears that the ratio of the growth rates averages about 10, while the ratio of uptake rates approaches 10 only at the lowest concentrations and decreases to 2 to 3 at 10^{-6} M. Thus, some slight synergism between IAN and IAA may perhaps be needed to explain the whole difference in growth activities, or alternatively the IAA which enters in the form of nitrile may perhaps reach its site of action with greater efficiency than when it enters as free IAA.

Summary

Avena coleoptile sections floated on solutions of 1-C^{14}-IAA or 1-C^{14}-IAN take up radioactivity rapidly for the first half hour and then at a nearly linear rate for 4 hours. The internal concentration in the tissue exceeds the external after 1 to 2 hours (depending on the absolute concentration), so that there is true accumulation. The uptake of IAA is about 5 times higher at pH 4.5 than at pH 7.5, while that of IAN is little affected by pH. Addition of unlabeled IAA actually promotes the uptake of labeled IAA. Much of the activity taken up in the first 30 minutes is lost again to unlabeled auxin or even to water; it is therefore considered to be in solution in the cell walls or other free space. This is supported by the fact that the initial uptake is not significantly decreased in purified nitrogen, although the susequent rate is about one half of that in air. This initial physical uptake is much larger with IAN than with IAA, and suggests that IAN may be concentrated in some lipophilic part of the tissue. At physiological concentrations, the rate of uptake of IAN is from 2 to almost 10 times as great as that of IAA, which explains most or all of the observed greater growth activity of the nitrile in Avena.

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