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An Attempt to Explain the Interaction of Auxin and Antiauxin in Root Growth by an Adsorption Mechanism

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The effects of auxins and their antagonists in root growth can be shown in diagrams, (*cf.* Åberg 1)) in which the molar concentration of the chemical compound in decadical logarithms is plotted against the observed root growth per cent of the root growth under normal conditions. S-shaped curves usually result, *e. g.* with 2,4-dichloro-phenoxyacetic acids; *cf.* also the full line curve in Fig. 1 of this paper.

Ass. professor Börje Åberg of this College drew the author's attention to this fact and pointed out that no attempts to explain the curve-form in mathematical terms have been published. This prompted the investigation described below.

It is not the author's intention to discuss the chemical processes connected with the retardation or acceleration of growth, but to describe the phenomenon in mathematical terms on the basis of the results obtained by Åberg.

The curves, given by Åberg for the phenoxy-acid mentioned above and other acids greatly resemble the curves for the dissociation of a weak acid; when pH is plotted against the fraction of acid dissociated. In this case $\alpha/(1-\alpha) = C_H + /k_s$ where k_s is the dissociation constant.

Another point, however, caught the author's interest. The equation above may be written

$$\frac{1}{\alpha} = \frac{k}{m} + 1 \tag{1}$$

It is identical with the Langmuir adsorption isotherm, α being the fraction of areas occupied in the adsorption pattern, m the concentration in solution.

The curve, Fig. 1 (full line), is actually the curve for the variables log m/k against α according to (1). As $m \rightarrow \infty$, $\alpha = 1$ *i. e.* saturation is reached.

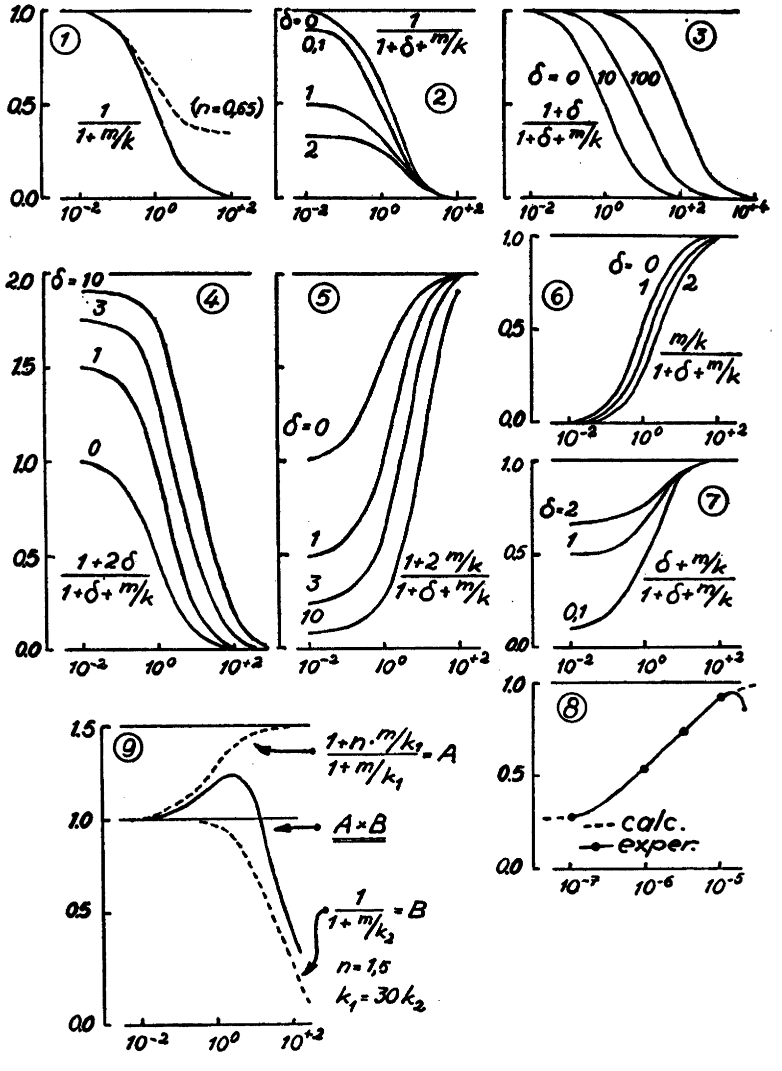

Fig. 1—9. The effects according to Table 1 and discussions in the text, of one component, Fig. 1, and combinations of two components, Fig. 2—8, in a single pattern p. 464 and in two patterns, Fig. 9, p. 467. Abscissa: m/k.

When $1/\alpha = 2$, semi-saturation is attained and at this point $m = k$ mole/lit. Thus the constant k is the concentration corresponding to $\alpha = 1/2$. Formally the constant corresponds to the concentration as a characteristic of the substance. It may be observed that the constant k is the only parameter of the equation and predicts the situation of the curve along the $1/m$-axis. The constant is referred to below as the constant of effect. For practical reasons its decadical logarithm, pk_v, is used.

Comparing the curve, Fig. 1 (full line), with those communicated by Åberg[1] for 2,4-dichloro-phenoxyacetic acid and α-indolylacetic acid the agreement in general is evident. Further the jump from 90 to 10 % effect, that is a jump in α from 0.9 to 0.1 occurs within two powers of ten in the concentration, that is also in m/k. This fact indicates a quantitative agreement. (Åberg's curves approach a value of 0.05 or 0.10 as $m \rightarrow \infty$, but the curve in Fig.1 tends to 0. This may be due to the fact that the root growth is not entirely regulated by the chemical used; *cf.* dotted curve in Fig. 1, referring to 65 per cent of the area available for adsorption.)

Thus, it seems possible to relate the retarding effect to an adsorption process. A corresponding process can be assumed for the accelerating effect and in principle a series of S-shaped curves should describe the growth process. Whether or not a chemical takes part in the biochemical processes, therefore, depends upon its concentration and constant of effect. Evidently an active chemical cannot produce any action if m/k does not rise to values markedly different from zero.

This rough picture can be submitted to further tests, for which some deductions from the Langmuir isotherm are needed, and are given below:

A system with one adsorbate gives:

$$\alpha_1 = \frac{m_1/k_1}{1 + m_1/k_1} = \frac{m_1/k_1}{M}$$

A system with two adsorbates gives:

$$\alpha_1 = \frac{m_1/k_1}{1 + m_1/k_1 + m_2/k_2} = \frac{m_1/k_1}{D}$$

$$\alpha_2 = \frac{m_2/k_2}{1 + m_1/k_1 + m_2/k_2} = \frac{m_2/k_2}{D}$$

A system with three adsorbates gives:

$$\alpha_1 = \frac{m_1/k_1}{1 + m_1/k_1 + m_2/k_2 + m_3/k_3} = \frac{m_1/k_1}{T}$$

$$\alpha_2 = \frac{m_2/k_2}{1 + m_1/k_1 + m_2/k_2 + m_3/k_3} = \frac{m_2/k_2}{T}$$

$$\alpha_3 = \frac{m_3/k_3}{1 + m_1/k_1 + m_2/k_2 + m_3/k_3} = \frac{m_3/k_3}{T}$$

Table 1. Combinations in systems with one and two components with activity (+) or none (0) in the free area and in the area occupied by the component.

Combination No.	Components	Activity in area	
		free	occupied
1 : a	1	+	0
2 : aa	1 2	+	0 0
2 : ab	1 2	+	0 +
1 : b	1	0	+
2 : ba	1 2	0	+ 0
2 : bb	1 2	0	+ +

The equations deduced can be connected with each other in many ways. Table 1 gives a summary of some combinations, whereby the free area is assumed to be active (+), or inactive (0).

In order to use the equations an assumption must be made regarding the connection between the state of adsorption and the growth. The most simple one is to put the growth (control L, experiment l) proportional to the free area, a. Thus $L \cdot c = 1$ and $l \cdot c = 1 - a$.

1 : a gives: $\frac{l}{L} = \frac{(1-a)}{1} = \frac{1}{1 + m/k} = \frac{1}{M}$,

i. e. the full line curve Fig. 1.

1 : b gives: $\frac{l}{L} = a = \frac{m_1/k_1}{1 + m_1/k_1}$, *i. e.* a mirror-image of the curve case 1:a.

2 : aa gives: $\frac{l}{L} = \frac{1-a_1-a_2}{1} = \frac{1}{D}$; m_1/k_1 may be written δ, thus $\frac{l}{L} = \frac{1}{1 + \delta + m_2/k_2}$, *i. e.* curves in Fig. 2.

2 : ab gives: $\frac{l}{L} = \frac{1-\alpha_1-\alpha_2+\alpha_2}{1-\alpha_0} = M_0 \cdot \frac{1+m_2/k_2}{D}$. (The subscript 0 refers to L.)

If m_2 is kept constant this equation may be written $\frac{l}{L} = M_0 \cdot \frac{1+\delta}{1+\delta+m_1/k_1}$. The curve for the last factor is given in Fig. 3. Assuming that the area occupied by the component 2 (Table 1) is twice as active as the free area, the curve in Fig. 4 is obtained. If the ratio between the constants of effect is 10, the limit is 0 when $m_1 \rightarrow \infty$, and $(1+10\delta)\,/\,(1+\delta)$ when $m_1 \rightarrow 0$.

If m_1 is kept constant one obtains $\frac{l}{L} = M_0 \frac{1+m_2/k_2}{1+\delta+m_2/k_2}$, (where $\delta = m_1/k_1$) and the curves in Fig. 5, assuming that the area occupied by 2 is twice as active as the free area.

2 : ba gives: $\frac{l}{L} = \frac{\alpha_1}{\alpha_2} = \frac{M_0}{m_0/k_0} \cdot \frac{m_1/k_1}{D}$.

If m_1 is kept constant the last factor has the form $\delta/(1+\delta+m_2/k_2)$ giving curves of the form shown in Fig. 2.

If m_2 is kept constant the last factor is $(m_1/k_1)\,/\,(1+\delta+m_1/k_1)$ giving the curves in Fig. 6.

2 : bb gives: $\frac{l}{L} = \frac{\alpha_1+\alpha_2}{\alpha_0} = \frac{M_0}{m_0/k_0} \cdot \frac{m_1/k_1+m_2/k_2}{D}$;

resulting in the curves in Fig. 7.

Application of the derived equations. The simple cases in Fig. 1, combination 1 : a and 1 : b, refer to chemicals with retarding and accelerating effects. In these cases proportionality is supposed between the fraction of free area and action; with retarding effect the occupied area is supposed to be inactive or much less active than the free area; with accelerating effect the reverse is supposed to be the case.

The simultaneous effect of two chemicals or one chemical with complicated effect, *e. g.* 3-iodo-benzoic acid [1], needs further discussion. In principle there are two possibilities. The first is, that one adsorption pattern is available and the chemicals compete for the available area, the other, that two adsorption patterns are available, each pattern with its separate effect upon the main result produced. The last case may refer for example to 1-naphtylsulfide-acetic acid, which gives an accelerating effect in low concentrations, in high a retardation (Fig. 9, full line curve). Patterns of this kind, of course, may or may not be present in or on the same adsorbent; the theoretical postulates are nevertheless valid.

Evidently the two possibilities do not exclude each other, but in order to prove the assumptions, they must, of course, be discussed separately.

Single pattern. Åberg found that 2,4-dichloro-phenoxyacetic acid in the presence of 1-naphtylmethyl-sulfide-β-propionic acid gave a normal curve, somewhat displaced at high values, comparable with the curves in Fig. 3.

With the value $m_1 = 2 \cdot 10^{-7}$, estimated from Åberg [3], and $k_1 = 4 \cdot 10^{-8}$ for the phenoxy acid from the equation valid for the curves in Fig. 3 (this paper) the value $\delta = 4$ is obtained. In this case, $m_2 = 1 \cdot 10^{-5}$, pk_v is 5.60. The concentration $m_2 = 2 \cdot 10^{-5}$ gives $m_1 = 4 \cdot 10^{-7}$ and pk_v = 5.66. Both experiments give the same value for pk_v = 5.6.

Another test may be performed using the G-values in Åberg's publication [3] (Table 11). The curve for $(1 + m/k) / (1 + \delta + m/k)$ being drawn for $\delta = 10^{-7}/4 \cdot 10^{-8} = 2.5$ and then being moved along the concentration axis until it most closely coincides with the experimental curve, we obtain with naphtylmethyl-sulfide-acetic acid Fig. 8, where the full line represents the experimental curve, the dotted line the calculated curve. The point $m/k = 10^0$ on the calculated curve is marked on the experimental curve by a point on the m/k-axis; this point, 6.35, is of course the pk_v value for the acid. Values determined in this way are given in Table 2 (I). In these calculations, as evident from the discussion, the retarding effect of the sulfide and selenide acids were disregarded, only the accelerating effect being taken into account.

Further, equation $(1 + m/k) / (1 + \delta + m/k) = l/L$ may be used for graphic representation. Using β for l/L one gets the expression log

Table 2. The decadical logarithm of the constant of effect, pk_v, *for some acids, calculated in two ways, (I) and (II), see text.*

No.	Substance	pk_v	
		(I)	(II)
a1	1-Naphtyl-methyl-sulfide-acetic acid	6.35	6.3
a2	2- » » » » »	6.5	6.3
b1	1- » » » -β-propionic acid	5.5	5.6_5
b2	2- » » » » »	6.1	6.0_5
c1	1- » » » -α-*iso*-butyric acid	*	(5.2) **
c2	2- » » » » » »	*	(6.4) **
d1	1- » » -selenide-acetic acid	6.7	6.6
d2	2- » » » » »	*	(6.3) **

* The curve given by Åberg [3] is a little obscure because of the strong retarding effect.

** Only one G-value could be used because of the strong retarding effect.

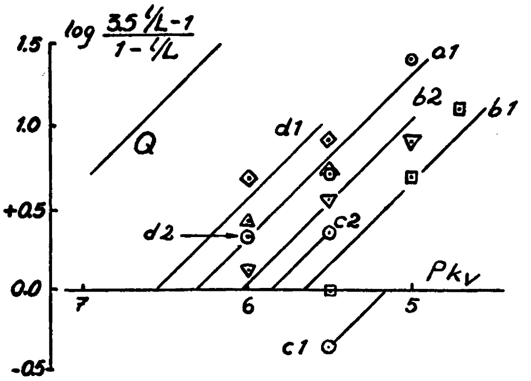

Fig. 10. Graphical evaluation of the pk_v *values for the acids, a1:* △ *, a2 (the same line as for a1): O, b1:* □ *, b2:* ▽ *, c1: 0, c2: 0, d1:* ◇ *and d2: (→) quoted in Table 2 and the theoretical slope (Q) according to deduction in text, p. 466—7.*

$(3.5\,\beta-1)\,/\,(1-\beta)+\log k=\log m$, where m and k refer to the sulfide- and selenide-acid respectively, and a straight line with the intercept pk_v on the log m-axis should be obtained. Of course only the G-values unaffected by the retarding effect can be used. Bearing this in mind we obtain Fig. 10, and the results may be taken as a verification of the postulates. The intercepts, *i. e.* pk_v values, are given in Table 2 (II).

The acids mentioned accelerate the growth above that of the controls, $l/L > 1$. This may be due to the fact that the activity of the areas occupied by them is higher than the activity of free areas (*cf.* Fig. 5). Such an assumption introduces a new parameter. Other deductions could also be made with the aid of the relations given in Table 1. In this case it seems necessary to discuss the presence of natural auxins and antiauxins, systems with three of even four actual components. In such a case so many parameters appear in the formulas that the discussion becomes rather unprofitable. The author therefore, concludes the discussion at this stage.

Multi patterns. A discussion of adsorptions in more than one pattern must be founded on some assumption concerning the manner in which they interact. If a single chemical promotes the growth at one concentration and represses it at another, finally causing complete inhibition, it seems obvious that the interaction cannot be expressed in terms of a sum. An interaction in the form of a product, on the other hand, seems more likely.

If this assumption is applied to the case where the accelerating and retarding effect is caused by a single chemical the following expression can be derived according to the equations given above: $\frac{1+n\cdot m/k_1}{1+m/k_1}\cdot\frac{1}{1+m/k_2}$ Fig. 9

gives the curves for each factor and for the product. The parameters chosen were $n = 1.5$ and $k_1 = 30\ k_2$. Other parameters, of course, give other curves, and obviously it is possible to construct curves valid for the experimental facts and the postulates. The curve in Fig. 9 undoubtedly gives satisfactory agreement with those given by Åberg[3].

Ultimately, combining the dotted line curve, Fig. 1, with a retardation in another pattern, the triiodo-benzoic acid curve given by Åberg[1] may be understood and discussed in a qualitative manner.

SUMMARY

The interaction of chemicals on root growth is difficult to interpret. It is shown that some simple mathematical deductions give surprisingly good agreements with experimental data.

The deductions may be founded on kinetical or adsorptionchemical conceptions. The latter especially were applied with the aid of the Langmuir adsorption theory. Adsorption in one pattern as well as in several (two) patterns have been discussed, and also the manner in which two (or more) patterns interact to produce the final result, here the root growth.

Applications should be made with caution, because with each assumption new parameters appear in the equations. Therefore no attempts have been made in this paper to discuss the presence of natural auxin or antiauxin.

Though caution is necessary, the author considers the ideas may be of value in this field as well as in the discussion of bacterial growth[4,5], enzyme action[6] and antagonism of drugs[7].

The author is indebted to ass. professor B. Åberg for stimulating discussions.

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