d'Amsterdam qui dispose d'un spectrographe à dispersion plus grande. Je tiens à remercier M. ZEEMAN de l'intérêt qu'il a pris à mon travail et M. DEBIERNE d'avoir mis à ma disposition les préparations d'actinium à étudier. Je remercie également M. VAN DER ZWAAL pour le soin qu'il a mis aux agrandissements des spectres.

Légende de la planche.

On trouve l'un au-dessus de l'autre, le spectre du produit 316 α 2 avec spectre du fer comme référence, le spectre du produit 317 et le spectre du produit 316 α 7 avec le spectre du fer.

Les raies du spectre de l'actinium sont marquées avec un point, et leurs longueurs d'onde indiquées.

Physics. — *Protoplasmic Movement in the Avena Coleoptile as related to Oxygen Pressure and Age.* By JOHANNA G. EYMERS and H. P. BOTTELIER. (Communicated by Prof. L. S. ORNSTEIN).

(Communicated at the meeting of June 26, 1937).

In a recent paper (1935) the second author described the influence of aging on the relation between temperature and protoplasmic movement in epidermic cells of *Avena* coleoptiles. The protoplasmic streaming in young coleoptiles, 72 hours old, has a $Q_5 = 1.05$ between 3° and 33°, while that in plants, 300—450 hours old, shows a VAN 'T HOFF curve corresponding with a Q_5 value of 1.33.

In intermediate stages the Q_5 has a high value (1.33) at lower temperatures, which at higher temperatures turns into the low value (1.05). As the plants grow older the temperature at which the "high value" curve passes into the "low value" curve regularly rises (fig. 1).

By changing the oxygen content of the water surrounding young and old coleoptiles we could prove (1935) that the oxygen concentration in the medium limits the rate of the protoplasmic streaming in those cases, where the $Q_5 = 1.05$. The facts mentioned simply can be explained by the hypothesis that the oxygen diffusion from the medium towards the protoplasm is the process with the low Q_5.

In the stages, investigated here, the growth of a coleoptile consists in cell elongation only (AVERY and BURKHOLDER, 1936), the length of the cells increasing considerably, while the amount of protoplasm practically remains the same. In a given unit of time more oxygen will diffuse into the larger cells of old coleoptiles than into the smaller cells of young coleoptiles. At a given oxygen pressure in the medium a given volume of protoplasm in the first case will get more oxygen than in the second. If this consideration duly explains the fact that the rate of protoplasmic movement in old coleoptiles is limited at much higher temperatures than in young ones, a relation between streaming velocity, oxygen concentration in the medium and cell surface can be deduced as follows.

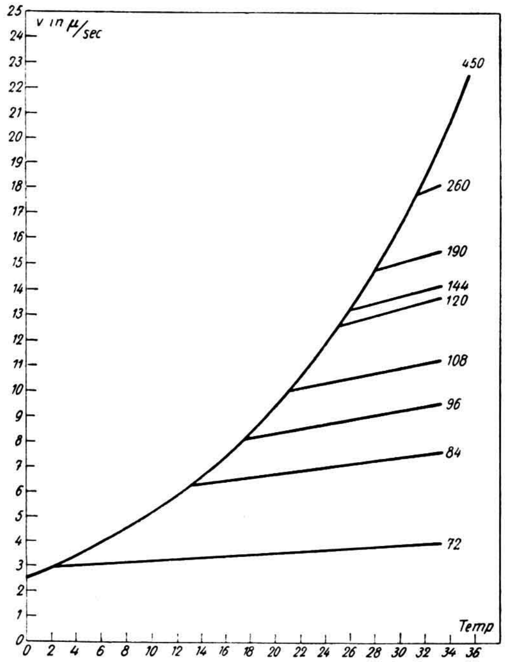

Fig. 1. Influence of the temperature on the velocity of protoplasmic streaming. The figures at each curve indicate the age of the coleoptiles in hours. VAN 'T HOFF curves with $Q_{\frac{28}{23}} = 1{,}33$ and 1,05 respectively. (After BOTTELIER, 1935).

The ratio between streaming velocity, measured at a given temperature in a coleoptile of a given age, and that in a coleoptile aged 450 hours at the same temperature is a measure of the oxygen deficiency of the coleoptiles of that given age. In the equation:

$$v(T) = f \cdot v_I(T)$$

$v(T)$ = the streaming velocity at a given temperature (T) at a given age and $v_I(T)$ = the streaming velocity at the same temperature, when oxygen is not limiting, i.e. in coleoptiles aged 450 hours. Now f indicates the lack of oxygen, depending upon: 1) the amount of oxygen available for protoplasmic movement per unit of protoplasmic surface and per unit of time, 2) the cell surface through which the oxygen has to diffuse. Therefore:

$$f = C \cdot Z \cdot \sigma$$

when Z = the amount of oxygen mentioned under 1); σ = cell surface. According to the definition given above, to C the value is given at which $f = 1$, if the streaming velocity is no longer limited by the oxygen concentration in the medium.

In this formula f and σ can be determined experimentally.

$f = \frac{v(T)}{v_I(T)}$ can be culculated from fig. 1. Table 1 represents the values of f at different temperatures and for different ages. In fig. 2 f for

TABLE 1. f-values at different temperatures for coleoptiles of different ages.

Age in hours / Temperature	72	84	96	108	120	144	192	264
2°	1.00							
4°	0.88							
6°	0.79							
10°	0.63							
13°	0.55	1.00						
15°	0.49	0.90						
18°	0.43	0.79	1.00					
20°	0.38	0.71	0.89					
23°	0.33	0.61	0.76	1.00				
25°	0.29	0.56	0.69	0.82	1.00			
26°	0.28	0.53	0.66	0.81	0.95	1.00		
28°	0.26	0.49	0.60	0.72	0.87	0.87	1.00	
30°	0.24	0.44	0.55	0.64	0.79	0.82	0.91	
31°	0.22	0.43	0.53	0.57	0.76	0.79	0.87	1.00
33°	0.20	0.39	0.47	0.53	0.69	0.73	0.80	0.92

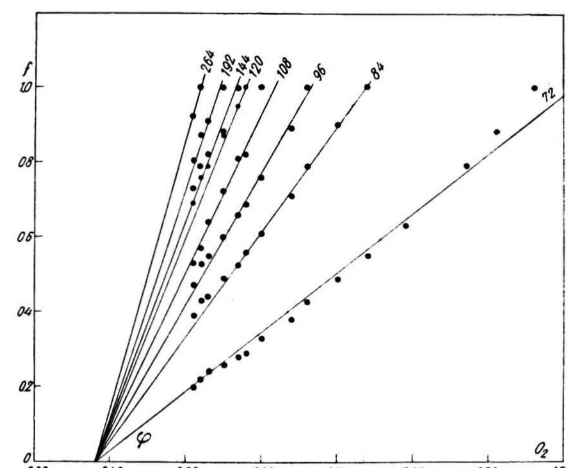

Fig. 2. Ratio of velocities of protoplasmic movement in old coleoptiles and in coleoptiles of different ages (f) plotted against oxygen concentration.

different ages is plotted against the oxygen content of the medium (according to LANDOLT and BÖRNSTEIN, 1923; see last column of table 3). From this figure can be derived, that $f = \varphi\ (O_2—0{,}38)$, where φ is depending on the age. When we compare this formula with that given above: $f = C.Z.\sigma$, we must conclude: $Z = O_2—0{,}38$ and φ must be proportionate to σ. From $Z = O_2—0{,}38$ follows $Z = 0$, when $O_2 = 0{,}38$, that means, that the protoplasmic movement in an *Avena* coleoptile stops as soon as the oxygen content of the medium falls below 0,38 vol. %, the amount of oxygen available for the protoplasmic movement (Z) then being 0. Fig. 3 gives φ as well as σ (the latter in relative values, derived from those of table 2), plotted against the age of the coleoptiles.

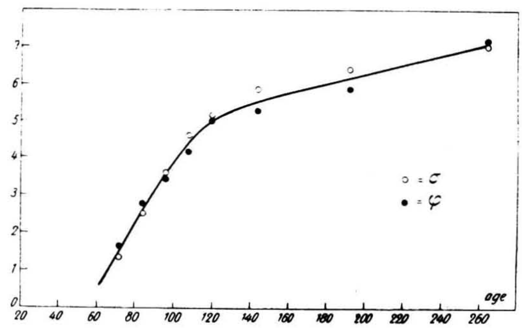

Fig. 3. The dependence of φ on the age and the increase of the surface of the cells (σ), which runs parallel with the φ-curve.

The figure shows that the values of both depend in exactly the same way on the age.

σ has been determined as follows. In all experiments mentioned above the protoplasmic movement has been measured in epidermic cells at 5—10 mm from the top of the coleoptile. The length and diameter of 10—20 cells in this region of coleoptiles of different ages was determined. The epidermic cells are longish bobbin shaped. In the approximate estimation of the cell surface they were supposed to be cylinders, the main diameter of each cell being used as diameter of the cylinder. The values obtained in this way run from 0.003 mm^2 in coleoptiles of 50 hours old to 0,137 mm^2 in 450 hours old ones. In table 2 the relative values are given, 0,137 mm^2 being put 100.

TABLE 2. Surface of epidermic cells 5—10 mm from the top of the coleoptile (relative values).

Age in hours	48	72	84	96	108	120	144	192	264	448
Surface (σ)	2	17	32	46	59	66	75	82	89	100

From the fact, that φ is proportionate to σ can be concluded, that our supposition: $f = C.Z.\,\sigma$ is correct. This supposition, however, can still be tested in a different way:

According to our postulate f for every temperature should be proportionate to σ as determined for the different ages studied. When now $\frac{f}{\sigma} = C.Z$ is calculated, for every temperature values must be expected independent of the age. Table 3 shows that $\frac{f}{\sigma}$ indeed is practically independent of the age for each temperature. If we had not divided by the

TABLE 3. *C.Z*-values at different temperatures for coleoptiles of different ages. O_2 = amount of oxygen (cm^3 0°, 760 mm Hg-pressure), dissolved in 100 cm^3 air-saturated water.

Age in hours / Temperature	72	84	96	108	120	144	192	264	mean	O_2
2°	0.059								0.059	0.96
4°	0.052								0.052	0.91
6°	0.046								0.046	0.87
10°	0.037								0.037	0.79
13°	0.032	0.031							0.032	0.74
15°	0.029	0.028							0.029	0.70
18°	0.025	0.025	0.022						0.024	0.66
20°	0.022	0.022	0.019						0.021	0.64
23°	0.019	0.019	0.016	0.017					0.018	0.60
25°	0.017	0.018	0.015	0.014	0.015				0.016	0.58
26°	0.016	0.017	0.014	0.014	0.014	0.013			0.015	0.57
28°	0.015	0.015	0.013	0.012	0.013	0.012	0.012		0.013	0.55
30°	0.014	0.013	0.012	0.011	0.012	0.011	0.011		0.012	0.53
31°	0.013	0.013	0.012	0.011	0.012	0.011	0.011	0.011	0.012	0.52
33°	0.012	0.012	0.010	0.009	0.010	0.010	0.010	0.010	0.011	0.51

cell surface (σ) but for instance by the length of the cells, the divider would have been larger for young cells than now and smaller for old cells. If we had chosen the cell volume the reverse would have been the case. In both cases no independence of the age would have been obtained.

$\frac{f}{\sigma}$ being independent of the age, for each temperature the mean value of $C.Z$ could be calculated and given in table 3. For temperatures below 15° only one or two values for $C.Z$ were available. In the last column of table 3 the amount of oxygen in vol. % is given, dissolved in air saturated water at the given temperatures (from LANDOLT and BÖRNSTEIN, 1923). If the mean *C.Z.* values are plotted against the amount of oxygen dissolved in water (fig. 4) a straight line is found. This line should reach the *X*-axis at the same O_2-value as the curves of fig. 2, namely at $O_2 = 0{,}38$. In fact 0,41 is found. This is a satisfactory accordance, since only the figures from 72 hours old plants are available for the higher values of the curve in fig. 4, the *C.Z.*-values for this age being somewhat higher than the figures, used for the other values. If in fig. 4 *C.Z* had been plotted against O_2 for each age separately, the accordance still

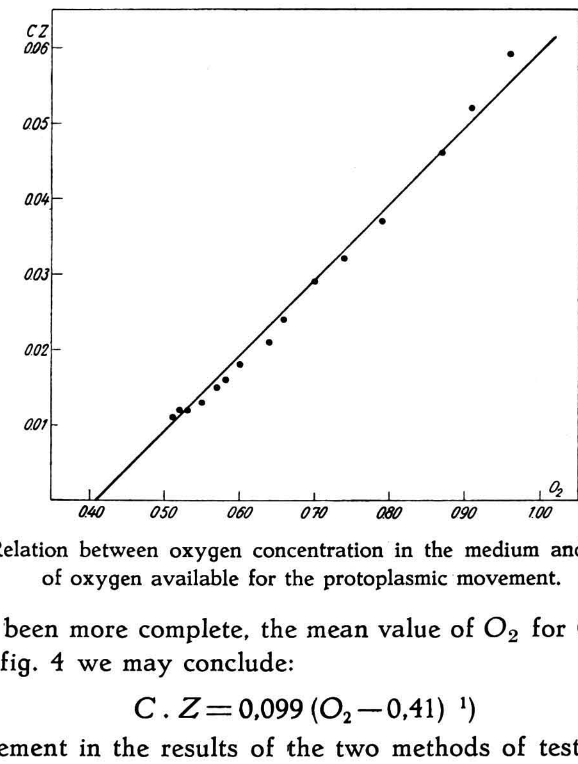

Fig. 4. Relation between oxygen concentration in the medium and the amount of oxygen available for the protoplasmic movement.

would have been more complete, the mean value of O_2 for $C.Z = 0$ being 0,37. From fig. 4 we may conclude:

$$C\,.\,Z = 0{,}099\,(O_2 - 0{,}41)\ ^{1})$$

The agreement in the results of the two methods of testing the supposition: $f = C.Z.\,\sigma$ is satisfactory.

On account of these considerations the velocity of the protoplasmic movement in an *Avena* coleoptile can be described by the equation:

$$v = 0{,}11\,(O_2 - 0{,}44)\,.\,\sigma\,.\,v_I$$

for oxygen concentrations where $0{,}11\ (O_2 - 0{,}44)\,.\,\sigma \leqq 1$.

[1]) From unpublished investigations by Miss M. W. MOL follows that, in the microthermostat after HILLE RIS LAMBERS (1926) used in our experiments, a diffusion resistance occurs between the coleoptile and the water flowing past it. This resistance being removed, the limiting effect of oxygen on the protoplasmic streaming in a coleoptile of a given age occurs only at much higher temperatures than in our cases. Part of the factor 0,44 therefore will come on the account of this diffusion resistance. This fact, however, does not interfere with the principles of the given reasoning.

When the medium is still richer in oxygen, oxygen diffusion is no longer the limiting process for the streaming velocity. v_I follows a VAN 'T HOFF formula:

$$v_I = A e^{-\frac{\alpha}{T}} = 3{,}4 \, . \, 10^8 \, e^{-\frac{5.1.10^3}{T}}$$

(A and α are calculated from the curve of fig. 1; $Q_{\frac{28}{23}}$ being 1,33).

A temperature-velocity curve for the protoplasmic movement always must be the result of the cooperation of at least two factors: changes in viscosity (η) of the protoplasm as well as changes in the force(s) causing the movement. A simple equation can be given as follows:

$$v_I = \frac{force}{\eta}.$$

For most liquids η agrees with a VAN 'T HOFF formula within the given temperature range. If one puts $\eta = Be^{\frac{\beta}{T}}$, the "force" then would be $v_I \, \eta = A \, . \, Be^{\frac{\beta - \alpha}{T}}$. If we knew η for the protoplasm of *Avena* coleoptiles, the force could be calculated by means of this formula. Parallel determinations of the respiration probably would give an answer to the question whether respiration and protoplasmic movement are really directly related or not.

SUMMARY.

Temperature-velocity curves of the protoplasmic movement in epidermic cells of young *Avena* coleoptiles are different from the VAN 'T HOFF curve shown by the protoplasmic movement in old coleoptiles (fig. 1). This difference is caused by oxygen deficiency in the cells. The curves entirely can be explained by assuming that 1) the oxygen concentration of the medium decreases with rising temperature, 2) the surface of the cell through which the oxygen has to diffuse increases with the age of the coleoptile.

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