sweeps with the pole, checking half-circle areas of 8-ft radius in front and to the side of him to detect the presence of the tagged animal. Activity of ½ mc in the capsule made it possible to determine the approximate location of the mouse when the Geiger-Müller tube was 3 or 4 feet away. The location of the animal was then determined within 3 or 4 inches by using the meter and headphones. The location of a tagged animal several inches below the surface of the ground could not be accurately determined with the equipment and level of activity used in this experiment.

Once the tagged mouse had been found the operator remained in position until the animal moved to another location. The first location was then marked by tossing a numbered pressed wood board, 4 by 4 inches, on the place to be marked. This method of marking made it unnecessary to approach and perhaps disturb the animal. After a tracking period of 1 or 2 weeks the location points were mapped by means of a surveyor's transit and tape. The tagged mice were recaptured at the end of the study period, and the capsules were removed. After removal of the capsules these animals were often retagged in the laboratory and released again for further tracking.

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26 February 1962

Prediction of Ultrafiltration Membrane Performance

Abstract. A theory for ultrafiltration is presented which makes possible the characterization of a membrane at a given temperature and solute concentration by a single experiment at that temperature and concentration. The theory is applied to data in the literature and is shown to be consistent with those data.

Ultrafiltration data show that salt rejection improves as the pressure across the membrane increases (*1–3*). Heretofore, no completely satisfactory explanation of this phenomenon has been presented. An explanation of the phenomenon with a demonstration of its application to experimental data is presented in this report.

Table 1. Summary of calculations of J, J', $\mu_1 - \mu_2$, and $\mu'_1 - \mu'_2$ from data of Ambard and Trautmann (*1*).

Pressures and compositions	J	J'	$\mu_1 - \mu_2$	$\mu'_1 - \mu'_2$
	Data			
$(p_1 - p_2)$, kg/cm²	0.9	2.2	3.5	4.4
Filtrate, ml/hr	37	90	136	168
Filtering solution, NaCl mg/lit.	100	100	100	101
Filtrate, NaCl mg/lit.	89	77	69	67
	Calculations			
Water flow, J g/hr	37	90	136	168
NaCl flow, J' 10^{-3} g/hr	3.29	6.92	9.39	11.2
n_1, 10^{-5} mole/mole	3.08	3.08	3.08	3.11
n_2, 10^{-5} mole/mole	2.74	2.36	2.12	2.06
$RT \ln(1 - n_1/1 - n_2)$, 10^{-3} cal/mole	−2	−4	−6	−6
$RT \ln(n_1/n_2)$, cal/mole	68.2	156	219	240
$\bar{v}(p_1 - p_2)$, cal/mole	0.38	0.93	1.49	1.87
$\bar{v}'(p_1 - p_2)$, cal/mole	0.4	0.9	1.4	1.8
$\mu_1 - \mu_2$, cal/mole	0.38	0.93	1.48	1.86
$\mu'_1 - \mu'_2$ cal/mole	69	157	220	242

The driving force for ultrafiltration is the chemical potential μ. If interference between components is negligible, the flow rate of each component is dependent upon the change in its own chemical potential as it passes from the solution on one side of the membrane to that on the other side and is directly proportional to the degree of change, to at least a first approximation. Then the rate of flow of solvent across the membrane is

$$J = (\mu_1 - \mu_2)/r \qquad (1)$$

where r is the resistance to flow of solvent. If the liquid phases are agitated sufficiently to make film resistances negligible, the major resistance to flow is offered by the membrane, and

$$r = d/D \qquad (2)$$

where d is the thickness of the membrane and D is a modified diffusion coefficient for the solvent in the membrane analogous to the Fick diffusion coefficient.

The analogy between D and the Fick diffusion coefficient can be seen by substituting Eq. 2 into Eq. 1, so that

$$J = [D(\mu_1 - \mu_2)]/d \qquad (3)$$

Equation 3 shows that D relates flow rate to chemical potential gradient, just as the Fick diffusion coefficient relates flow rate to concentration gradient.

The available data show only that D and r do not vary appreciably over a limited pressure range. Variation with temperature, concentration, or other factors remains to be determined.

Similarly, the rate of flow of a dissolved component is

$$J' = (\mu'_1 - \mu'_2)/r' \qquad (4)$$

At constant temperature, the chemical potentials depend upon pressure and the amounts of the dissolved materials present. The resistances remain constant over wide ranges of pressure.

Experimental data from Ambard and Trautmann (*1*) which demonstrate improvement in salt rejection with increase in pressure are shown in Table 1, rows 1 through 4. Calculations based on these data make up the remainder of the table. A temperature of 21°C was

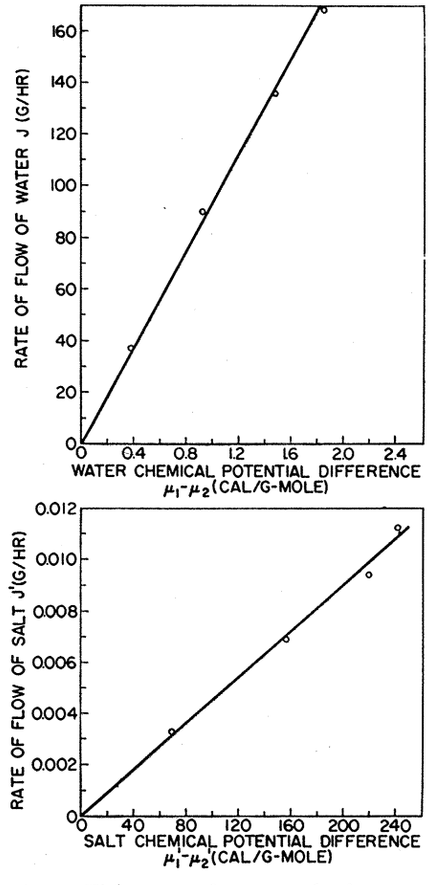

Fig. 1. Flow rates of water and salt across an ultrafiltration membrane as functions of the respective chemical potential differences across the membrane. [From data of Ambard and Trautmann (*1*)]

assumed. A value of 18 ml/mole was used for the partial molal volume of water and a value of 17.1 ml/mole, for the partial molal volume of sodium chloride (*4*).

For the range of pressures and compositions in Table 1

$$\mu_1 - \mu_2 = RT \ln[(1 - n_1)/(1 - n_2)] + \cdot \bar{v}(p_1 - p_2) \quad (5)$$

and

$$\mu'_1 - \mu'_2 = RT \ln(n_1/n_2) + \bar{v}'(p_1 - p_2) \quad (6)$$

where n_1 and n_2 are the mole fractions of NaCl on each side of the membrane, $\bar{v}$ is the partial molal volume of water, $\bar{v}'$ is the partial molal volume of NaCl, and p_1 and p_2 are the pressures on each side of the membrane.

In Fig. 1, J has been plotted against $\mu_1 - \mu_2$, and J', against $\mu'_1 - \mu'_2$. In each case the data can be represented by a straight line through the origin; this shows that the resistances are constant over the ranges of pressure and concentration given in Table 1. The resistance is the reciprocal of the slope of the line.

The calculations in Table 1 show that

$$RT \ln[(1 - n_1)/(1 - n_2)]$$

is small as compared to $\bar{v}\ (p_1 - p_2)$ for the range of data presented. So the rate of flow of water in effect is proportional to the pressure across the membrane. Conversely, values of $\bar{v}'\ (p_1 - p_2)$ are small as compared to

$$RT \ln(n_1/n_2)$$

so the rate of flow of NaCl depends primarily on the concentration of NaCl on each side of the membrane. At low pressures, water flow is low and salt rejection appears poor. At higher pressures, water flow is higher and salt rejection appears improved. Mahon (*3*) pointed out that water flow was dependent on pressure, and salt flow, on concentration, but he gave no reasons for such dependence.

Data over wider ranges of pressure, membrane thickness, and concentration are necessary to establish the limits of application of the theory introduced here. Within these limits it will be possible to predict a membrane's performance in ultrafiltration, for different thicknesses, pressures, and concentrations, from experiments yielding the values of the various modified diffusion coefficients through the membrane.

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Inter-tissue Complementation: A Simple Technique for Direct Analysis of Gene-Action Sequence

Abstract. Sequence of gene action can be determined from unidirectional complementary interactions between synthetically active but genetically blocked tissues. A linear sequence of gene action has been constructed for anthocyanin synthesis in maize by this approach. This technique probably can be applied to other systems and organisms that have the requisite circumstances.

Application of modern biochemical methods to the many phenotypically established genetic systems in higher organisms can be aided by simple methods for the determination of gene-action sequence. A disarmingly simple prediction can be made that biochemical interactions will occur between excised tissues of complementary genotypes. This prediction is based on the known accumulation of intermediates preceding a genetic block (*1*) and of the utilization of appropriate intermediates by living tissues (*2*). Although these interactions would be analogous to those found in tissue transplants with *Drosophila* and in cross-feeding in microorganisms, they are predictably unidirectional and the results would permit direct determination of gene-action sequence. This report describes such experiments in maize, establishing the sequence of gene action in anthocyanin synthesis.

Anthocyanin synthesis in the aleurone tissue of maize is controlled by several known complementary genes, several modifiers, and a dominant inhibitor, which variously block, reduce, or enhance the formation of pigment. The presence or absence of anthocyanin pigment in this tissue is controlled by the complementary factors A_1, A_2, C_1, C_2, and R, which must be present in dominant condition for the production of anthocyanin. If any one is homozygous recessive or if dominant C^I is present, colorless aleurone results. The factors Bz_1, Bz_2, Pr, and In determine the intensity and the nature of anthocyanin. Previous investigations (*3–6*) have indicated that these factors act in a step-wise manner in the formation of anthocyanin. A gene-action sequence based on indirect reasoning from interactions has been constructed, but it was pointed out that direct studies with active synthetic stages were needed (*7*).

McClintock (*8*) observed that complementary pigment synthesis occurs at the line of contact between genetically colorless (inhibited) C^I Bz cells and nearly colorless (bronze) C bz cells. The relation of this observation to the diffusibility of anthocyanin precursors and to the sequence of gene action has been discussed by Rhoades (*5*). These considerations led to the present repetition of these effects in vitro with excised tissues of complementary genotypes.

The individual testers, a_1, a_2, c_1, c_2, r, bz_1, bz_2, and in, all singly recessive, and homozygous C^I were grown and self-fertilized. In the period 22 to 25 days after pollination, when the tissue would be actively synthesizing pigment if it were genetically competent, aleurone tissue was peeled from fresh kernels. Two distinguishable pieces of different colorless mutants were pressed together and the pair was placed on 0.8 percent agar at 25°C. The results can be illustrated by a specific example: When a_1 and a_2 tissues are pressed together, complementary interaction results in anthocyanin synthesis in 1 to 2 days and is unidirectional—that is, only the a_1 tissue (the "receiver") develops pigment while the a_2 ("donor") tissue consistently remains colorless, as also do control tissues. The pigment was regularly confirmed to be anthocyanin by the standard test with dilute acid. These results clearly suggest that diffused substrate from the donor is used by the receiver to synthesize anthocyanin and that the block in the donor succeeds that in the receiver. The receiver of course would need to carry the dominant factor lacking in the donor as well as the subsequent factors in the sequence.

The "donor-receiver" relation is interchangeable and varies with the combination of mutants. For example, a_1 tissue, receiver in a_1-a_2 combinations, becomes a donor in a_1-r combinations. In any two paired mutant tissues only one develops pigment and the other never does, indicating that little or no diffusion of the pigment occurs from