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Matric Potential of Several Plant Tissues and Biocolloids[1]

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Summary. The pressure membrane apparatus was used to study the matric potential (imbibition pressure or moisture tension) of plant tissues and of several organic colloidal preparations.

The moisture release curves of aqueous 2 % agar, 12 % gelatin, and filter paper were smooth parabolic curves between matric potentials of −0.1 and −15 bars. When logarithms of the matric potentials were plotted against logarithms of the moisture content, the data yielded straight lines for agar and filter paper.

Slices of fresh tissue lost little water after 2 days in the apparatus at maximum pressure of 15 bars. Osmotic forces in conjunction with cell membranes are able to retain moisture against pressure of this magnitude. After the cells were disrupted by freezing and thawing, up to 90 % of the original moisture was removed by a 15 bar pressure, with lesser amounts removed at lower pressures. The results gave a parabolic relationship, and straight lines could be fitted to log — log plots of data from potato tuber and young asparagus stem slices. Sections from the tips of asparagus stems held less moisture at all matric potentials than more basal sections.

The method permits the study of the matric potential of tissues independently of the osmotic potential. As measured, however, the matric potential is a composite of matric potentials of colloidal substances in the protoplasm and cell walls after disruption of cells by freezing and mixing of the contents. The value is therefore only an approximation of the matric potentials occurring in the living tissues.

The condition of water in plant cells can be described in terms of the relationship

$$\psi = \psi_\pi + \psi_p + \psi_m$$

in which ψ is the water potential, ψ_π the osmotic potential due to solutes, ψ_p the turgor pressure or pressure potential, and ψ_m the matric potential due to adsorptive forces of colloids. The relative contributions of the osmotic and matric potentials to the water potential have not been extensively studied. Instead, in most discussions on the water relations of mature, vacuolate cells, it is tacitly or explicitly assumed that the adsorptive forces are quantitatively of minor importance relative to osmotic forces, and often they are not mentioned.

The rationale for neglecting the contribution of surface forces in discussions of the diffusion pressure deficit (DPD) is that the proportion of cytoplasm is small in the vacuolated cells which are generally chosen for discussion and that the contribution of adsorptive forces would therefore be minor. Also, it is commonly observed that when frozen tissues (e.g., vegetables purchased from the grocery store) are allowed to thaw, a considerable portion of the plant sap drains away in response to gravity alone. The water retained against gravitational force in such thawed material would presumably be held by adsorptive forces. If the thawed tissue is subjected to pressure in a hydraulic press, most of the water is pressed out, leaving only a moist residue. These observations suggest that on a quantitative basis, surface forces account for a minor, if undetermined, portion of the cells' water potential.

In soils, by contrast, surface adsorptive forces, generally here called soil moisture tension, pF, or matric potential, provide the major waterholding force in the soil as it dries. Only when the salt content of the soil is elevated do osmotic forces become relatively more important.

The pressure membrane apparatus has long been used for measuring the matric potential, as distinct from osmotic potential, of soils at various soil moisture contents, i.e., for determining the water release curves of soils (6, 7, 9, 10). This paper reports the use of this apparatus in determining the matric potential and water release curves of several biological colloids and plant tissues.

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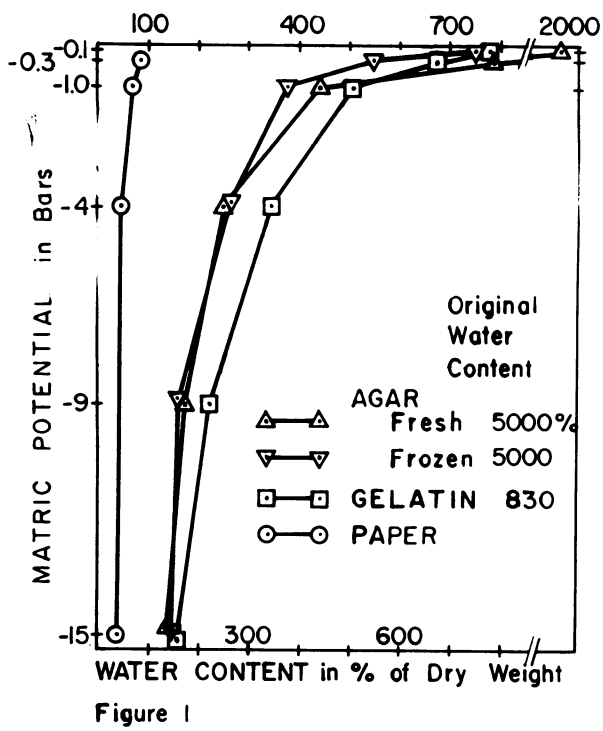
Materials and Methods

Fresh potatoes, *Solanum tuberosum* L., and asparagus, *Asparagus officinalis* L., were purchased from local (Stuttgart, Germany) grocers. Mangels or feed beets, *Beta vulgaris* L. were purchased in spring from local farmers after storage overwinter in underground caches. Potato tubers and mangel roots were peeled and cut into slices about 1 cm thick, placed in single layers in plastic bags into a deep freeze at −34° for 24 hours, or longer until needed. Enough sections were cut at one time, from a single mangel root or a given batch of potatoes and stored in the deep freeze until needed for determinations to be made at each particular pressure on successive 2-day intervals. The asparagus shoots were peeled leaving a square tapering core from which 4 sections were cut, with approximate measurements from the apex: 1, (apical section) 0 to 6 mm; 2, 6 to 15 mm; 3, 15 to 25 mm; and 4, (basal section) 100 to 110 mm. These sections were also frozen at −34° until used.

Moisture release curves were also determined for aqueous 2 % agar gel and aqueous 12 % gelatin gel, both prepared with boiling water, and for filter paper.

The pressure membrane apparatus used was of commercial manufacture, similar to that described by Richards (8). Dialysis membranes, type Lsg60, were purchased from Membranfilter GmbH, Göttingen, Germany. Nylon cloth was used instead of metal screen to provide drainage under the membrane.

The following procedure was used to determine the water content associated with a particular matric potential: The apparatus, nylon drain cloth, and membrane were assembled. The frozen or fresh plant material or agar was placed on the membrane, covered with a layer of sheet rubber and then with the sponge rubber, to insure good contact between tissues and membrane. The lid was closed and tightened, and compressed air was admitted to the apparatus. The entire assembly procedure required less than 5 minutes. Selected pressures ranging from 0.1 bar (Kg/cm^2) to 15 bar were used, and were each applied for 48 hours. Sap, or water from the agar, began to run out of the drain within a few minutes (or after frozen materials thawed). The initial rapid rate decreased after about 6 hours. In most instances no water could be collected after 24 hours and it is presumed the materials were near equilibrium with that particular pressure. After 48 hours the materials were removed, placed in tared stoppered bottles, weighed, oven dried at 105°, and reweighed to determine the water content as a percent of the dry weight. Microorganisms thrived on the tissues, so results obtained on materials left in the apparatus for more than 2 days would be doubtful validity.



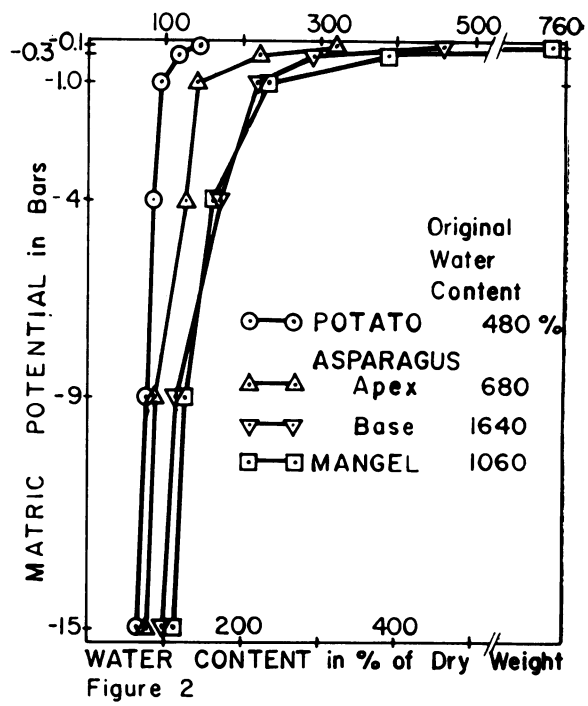


FIG. 1. (left) Water content of several biocolloidsas a function of the matric potential.

FIG. 2. (right) Water content of frozen and thawed potato tuber, mangel root and asparagus stem tissues as a function of the matric potential.

Results

The water retention of agar at various matric potentials is given in figure 1. As the pressure was progressively increased, less and less water was held by the agar. The logarithms of the matric potential, when plotted against the logarithms of the water content, give a straight line, and the data conforms to the Freundlich adsorption equation (2, 10).

About 140 % water remained in agar which had been in the pressure membrane apparatus for several days at 15 bar pressure. Contact with the membrane prevented lateral shrinkage, so water loss was accompanied by decrease in thickness. Agar at this moisture content feels only slightly moist to the touch, and is flexible or pliable, somewhat resembling leather. It becomes brittle at moisture contents below 50 %.

In a serial variation of the procedure, agar and thawed potato sections were subjected at successive 48 hour intervals to stepwise pressure increases. Samples were taken at 24 hour intervals for dry weight determinations. At each pressure increase, water moved out until a new equilibrium was reached. The results were identical to those reported in figure 1. Microorganism growth makes this method generally unsatisfactory.

At matric potentials between 0 and −1 bar, the frozen and thawed agar consistently held less water than unfrozen agar. At lower matric potentials of −4 bar or less, the water contents of thawed and of unfrozen agar were about the same. When agar is frozen and thawed it becomes spongy, filled with air bubbles, and water conductivity is reduced. Consequently, thawed agar loses water only slowly in the pressure membrane apparatus unless it is continuously pressed against the membrane by the sponge rubber pad mentioned earlier.

Gelatin and filter paper gave water release curves similar to those of agar. Filter paper held much less water at all potentials.

Living (unfrozen) tissues showed little change in moisture content after 2 days in the pressure membrane apparatus at 15 bars pressure (table 1). Intact cells, with membranes and osmotic substances are able to retain most of their water against a pressure differential of this magnitude.

After the cell membranes had been disrupted by freezing and thawing, the plant materials readily lost sap. Their moisture retention curves resemble those of agar (figure 2). Tissues with a matric potential of −15 bars contained on the average only about 10 % of their original moisture. Log — log plots of the data gave straight line relationships for potatoes and asparagus, and a curvilinear relationship for mangels. The starch grain content of the potatoes probably accounts for their lower water holding capacity, compared to the other tissues. The apical, more meristematic sections of asparagus shoots held less water at all potentials than did the more basal sections with vacuolated cells. Intermediate sections, 6 to 25 mm from the apex, retained intermediate amounts of water and are not reported in figure 2. Most of the difference in water retention occurred between 0 (living) and −0.1 bar MP, and could probably be associated with membrane disruption on freezing, and loss of vacuolar sap.

The solutes extracted from the thawed mangel root were studied briefly. The freezing point depressions, refractive indices, and conductivities of different fractions did not change appreciably or with any consistent trend, and were similar to those of sap extracted from thawed tissue by a cylinder and piston apparatus in a hydraulic press. Neither was there any consistent trend when the tissues were extracted by 6-hour, stepwise increases to 0.1, 0.3, 1.0 and 15 bar pressures. The osmotic pressures of the sap from different mangel roots ranged from 14 to 20 bars, as determined by freezing point depressions.

Since the membrane used is permeable to sugars and salts, the dry weight basis changes. Refractometer readings on extracted mangel sap gave sugar contents ranging from 3.5 to 8.0 %. A sugar content of 5 % was used to calculate approximately the grams of residue (R) per 100 grams of dry material.

Table I. *Moisture Content of Frozen and Thawed Beet Tissues as a Per Cent of the Measured Dry Weight and of Non-Soluble Residue.*

Ψ_m	A original % H_2O	B colloidal residue % of dry wt*	% H_2O adjusted A/B
0	1066 %	46.6 %	2290 %
−0.1	752	62.4	1210
−0.3	389	80.5	484
−1.0	233	88.3	264
−4.0	162	91.9	176
−9.0	127	93.6	136
−15.0	111	94.9	118
−15 living	1012	49.4	2050

* Residue = 100 − (0.05) (original % H_2O).

$$R = 100 - (.05)\ (\%\ H_2O)$$

These values are given in column 3 of table I. The moisture content as a percent of the nonsoluble dry weight is given in column 4. In fresh mangel tissue, more than 50 % of the dry weight is attributable to solutes and a recalculation of the percent moisture on a non-soluble residue basis gives a value more than twice that of the original value. At lower matric potentials, i.e., at lower moisture contents, this correction is less important, accounting for less than 10 % change at −15 bar. Since the insoluble residue consists of proteins, cellulose, and other colloidal substances, it is the fraction which is active in the surface binding of water, and there would be considerable justification for expressing the water release curve on this basis rather than on dry weight.

Discussion

The moisture release curves for biological colloids and frozen plant tissues appear qualitatively similar to those of soil colloids (6, 9, 10). They also resemble the moisture retention curves obtained by other techniques (1, 2, 3, 4, 5). In the energy range covered, −0.1 to −15 bars, there is no indication of a sharp break in the relationship between matric potential and water content, and the data generally fit the Freundlich adsorption equation.

The matric potential of the frozen plant tissue is a composite of the matric potentials of the various cell components. The moisture release curve of cell wall cellulose would be expected to differ from that of protein just as the curves of paper, agar and gelatin differ from each other. Each species of colloid would be expected to have its own unique moisture release curve, although the curves of related proteins might be similar. It is also possible that the disruption of cell structure would result in changes in the matric potentials of the components. After freezing the vacuolar solutions and cytoplasm mix and permeate the cell wall. The influence of ions from the vacuole on the structure and the matric potential of cytoplasmic and cell wall colloids awaits further study. Freezing itself may alter the moisture release curve of cytoplasmic colloids, as was found to be the case with agar. With reservations then, it is proposed that the moisture release curve obtained from frozen tissues represents a first approximation of the composite moisture release curve of the colloidal substances comprising the tissue.

On the basis of the moisture release curves, the quantitative contribution of matric potential toward the water potential of the tissues can be calculated. At a water potential of about −15 bars, which approaches wilting range, it is estimated that tissues such as the storage roots or asparagus stems used would have lost from 5 to 20 % of their fully turgid moisture content. Yet a matric potential of −0.1 bar is not approached until these same tissues have lost at least 50 % of their original moisture content. So in a tissue with a water potential of −15, the matric potential would be between 0 and −0.1, much smaller than the osmotic potential of the tissues, which often ranges around −10 to −25 bar.

The ψ_m of the tissues reported above did not approach −15 bar until only about 10 % of the original moisture content remained. The vegetative tissues of only a few vascular plant species can survive drying of this degree, or even loss of 50 % of their moisture. Such desiccation would also result in a 10-fold increase in osmotic potential, barring precipitation of solutes, with probable salting out of proteins. It is probably safe to conclude that cytoplasmic colloids do not contribute a quantitatively significant portion of the composite water potential of the tissues studied. The matric potential would probably be of greater importance in tissues of higher colloid content, such as seeds, meristems, and leaves.

Acknowledgment

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