ROLE OF WATER POTENTIAL IN MICROBIAL GROWTH AND DEVELOPMENT OF PLANT DISEASE, WITH SPECIAL REFERENCE TO POSTHARVEST PATHOLOGY[1]

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The subject of water relations in microbial growth and development of plant disease has been reviewed extensively (11, 13, 14, 18, 19, 28, 34), as has the subject of water relations of wood decay and growth of wood-decay fungi (20). This paper will not duplicate earlier reviews, except as necessary to present some basic principles. Our paper has 5 parts: 1) the water potential concept; 2) methods to measure water potential; 3) water potential requirements for growth of bacteria and fungi; 4) water potentials of the tissues of some fruits and vegetables after harvest; and 5) water potential and the development of disease.

The water potential concept

Numerous concepts and associated terms have been developed to describe and quantify the water to air, plant tissues, soil and other places. For example: vapor pressure and relative humidity refer to water in air; water activity is used to express the water in seeds and dried foods; osmotic pressure, turgor pressure, and diffusion pressure dificit have been used for the water in living plant tissues; and field capacity and permanent wilting point have been used for the water in soil. For the growth and activity of microorganisms and for most if not all cellular functions, the important water consideration is the relative energy status of the water. *Water potential* is an expression of the energy status of water. The energy of water determines water availability for life processes.

Water potential is a short way to say: "the potential energy of water." For most applications, pure free water is assigned zero potential energy, meaning that it has zero work capacity relative to water not pure or free. Water less than pure and free has a negative potential energy; water under pressure (e.g., turgor water) has positive potential energy. As the water potential decreses, it becomes less available. The unit of water potential used most commonly in soils and plant literature is the bar (1 bar = 100 Joules/kg = 0.987 atm). Since water in air is generally less than 100% relative humidity (rh), and that in microbial and plant tissues (including fruits) is not pure or free, the water potentials of concern with plants, microorganisms, and soil are almost always negative. Nevertheless, all water, whether in soil, cells, tissues, or air at uniform temperature can be expressed in terms of its potential energy, and thus water potential provides a simple and common language for scientists working with water.

The convenience and simplicity of water potential as an expression of the water status of a system are illustrated in Fig. 1 for a hypothetical fruit within a hypothetical storage bin. The water potential (ψ) of the fruit is the sum of the water potential components in the fruit cells, i.e. primarily an osmotic potential (π), but possible also a pressure or turgor potential (P). The water potential in equilibrium with the rh of the atmosphere around the fruit is calculated from $\psi = (RT/V)\ ln$ rh (Eq 1), where R is the ideal gas constant, T is absolute temperature, and V is the volume of a mole of water. Table 1 gives some conversion values between water potential and rh calculated for 25°C.

Water flows from areas of high to areas of low water potential, until energy equilibrium is reached. We can generally assume that the water potential of a fruit will be higher, on the average, than the equilibrium rh of the surrounding atmosphere (Fig. 1). Thus, the fruit will lose water to the surrounding atmosphere, although this process might be greatly slowed if the skin of the fruit is a sufficient barrier to water flow. Knowing the water potential of the exact site occupied

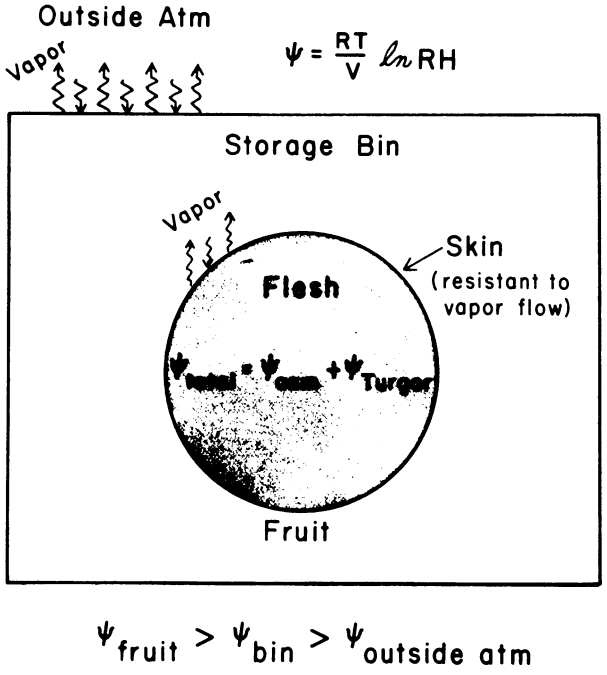

Fig. 1. Diagrammatic illustration of a hypothetical fruit in a storage bin showing relationships and components of water potential in such a system.

by a microorganism (in the fruit, on the skin, or in the air) has prediction value in terms of whether or not growth is possible for that microorganism.

The advantage of using the water potential concept to express the availability of water for microbial growth and other cellular processes is that the component potentials contributing to the total can be readily separated to distinguish between the different forces acting on the water. Within and between the cell walls and in conductive tissue, water is essentially solute free and is subjected to tension and adsorptive forces from the wall matrix. This effect on water is termed matric potential (τ). Where walls are not completely rigid, the water energy is lowered further by a deformation potential (D) from pressure and tension forces acting to deform the wall matrix. Inside the intact cell, the constitutents are highly hydrated (therefore $\tau \sim 0$), so the water potential of the symplasm is the sum of the osmotic potential (due to solutes) and the turgor potential (due to the presence of the semi-

Table 1. Equilibrium relative humidities at different water potentials calculated for 25°C.

Relative humidity (%)	Water potential (bars)
100	0
99.8	−2.8
99.6	−5.5
99.0	−13.5
98.0	−27.8
92.0	−115
80.0	−307
50.0	−955
20.0	−2216

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permeable membrane). At equilibrium, the potential of the water inside the cell must exactly equal the potential of the water outside, hence $\psi = (\pi + P) = (\tau + D)$ (Eq. 2).

Methods to measure water potential

Numerous methods have been developed to measure plant tissue water potential or the components thereof (4, 37). Thermocouple psychrometry and the pressure bomb appear best suited for most studies. With these techniques, it is important to understand clearly what is measured to avoid misinterpretation of tissue water parameters. In most work, the emphasis on measurement has been with leaves or stems of the plant and very little with storage organs.

The pressure bomb measures the tension of water in xylem. An excised plant part, usually a full leaf or the entire above-ground portion of a plant is placed in a chamber with the cut end exposed to the atmosphere through a pliable seal. Air is introduced into the chamber from a compressed source until water extrudes at the exposed cut end. The water potential is taken as the negative of the pressure applied to force the water out. Pressures to force water out of plant leaves may range from less than 5 bars for fully turgid tissue to more than 40 bars for certain species and depending on stress conditions. A correction for the osmotic potential of the xylem sap is sometimes made, but this usually is less than 0.5 bar.

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The pressure bomb offers a relatively simple, rapid, and easy-to-use method to obtain plant water potentials in the field and in controlled environments. Sensitivity of measurement in most application is within 1/3 to 1/2 bar, which corresponds to rh changes of about 0.02 or 0.03%. Procedures for use of the bomb are well developed for numerous plant species (5,6,16,17,24,33). Limitations of this technique are with physical dimensions of tissue materials (e.g., large fruits and vegetables, large leaves or stems, woody plants) which may require specially designed equipment to contain the organ or to seal the protruding surface against the atmosphere.

With thermocouple psychrometry, water potential is inferred from measurement of the equilibrium rh using Eq. 1. Sensitivity of measurement by psychrometry is 0.3 to 0.5 bar between −2 and −60 bars. This method is insensitive in the very wet (0 to −2 bar) range. Water potential may be determined *in situ* or with expressed sap from tissue. With *in situ* measurements, a small chamber with a built-in thermocouple element is sealed to a leaf surface and the equilibrium rh of the air in a small space above the leaf is determined (9,23); Crucial to the measurement is vapor equilibrium, which in the field is often a problem because of temperature fluctuations.

Measurements with excised tissue using psychrometry are usually made on samples brought to the laboratory. Vapor equilibrium is established with tissue water within a sealed chamber, and the rh is determined as with the *in situ* measurements. One difficulty with this method is in establishing a reproducible equilibration period, because of changes in metabolic processes associated with the excision itself (28).

In some cases, the osmotic potential of the cell contents can be estimated using expressed tissue sap placed in the chamber of a thermocouple psychrometer unit. For this measurement, the tissue must be killed (cell membrane destroyed). Sap expressed from living tissue is subject to filtration from the semipermeable membranes, which causes high values of π. Killing the tissue by exposure to liquid N or CO_2 ice destroys the membranes and allows cell contents to be expressed with only slight pressure. Also for this measurement, the tissue must not contain a high fraction of apoplastic water; such solute-free water will dilute the cell sap so that readings may give erroneously high values of osmotic potential. The apoplastic water may be 20 to 30% of the water content of some plant leaves, but appears to be much lower and possibly insignificant for storage tissues such as potatoes (G.S. Campbell and R. I. Papendick, unpublished data).

The osmotic potential of the cell sap gives an estimate of ψ when the turgor potential is low, such as during days of high stress or under conditions of low soil moisture.

Direct measurement of turgor potential is difficult and hence is usually computed from Eq. 2, knowing ψ and π. Recently, a specialized tecnhique using a hydraulic press has been developed for measurement of matric potential in plant tissue (35).

Water potential requirements for growth of bacteria and fungi

In general, bacterial and fungal growth are maximal in the range of −3 to −5 bars water potential, and growth is prevented, or nearly so, in the range of −40 to −50 bars water potential. Bacteria, in particular, (Table 2, Fig. 2) and fungi such as *Pythium* spp. (Fig. 3) require the highest water potentials for growth and are generally prevented from growing if the water potential drops below −30 to −40 bars. In contrast, fungi such as *Fusarium* (11) can grow at water potentials down to −100 to −120 bars, and some species of *Aspergillus* (Fig. 4) and *Pencillium* can grow at water potentials down to −200 to −250 bars, possibly even lower (34). There is also evidence (1,15) that lowering the osmotic potential is less limiting to growth of fungi than an equivalent lower of matric potential. For most microorganisms, the exact water potential requirements are still unknown, but the evidence available indicates that every microorganism differs from every other microorganism in water potential requirements. Moreover, the requirements of a given organism vary with temperature (11) (Table 2), pH (Fig. 2), and probably many other factors. In general, the more favorable the nutrition and environment, the lower the water potential at which the microorganism can grow.

Some terms used to classify microorganisms (34) according to water requirements are halophilic (applied to bacteria with a high salt tolerance), osmophilic (applied mainly to yeast with ability to grow in relatively high concentrations of sugars), and xerophilic (applied mainly to fungi with ability to grow under or even a preference for dry conditions). The common feature of the organisms classified by one or another of these systems is an ability to grow at low water potentials.

Bacterial cells and fungal hyphae have a water potential that, like other cells, includes mainly the osmotic and turgor components. Cells in a active state of growth are presumed to have a total water potential at or slightly below that of the site they occupy (ψ microbial cell < ψ environment of cell). If the ψ microbial cell is slightly lower than that of the surrounding environment, water will flow into the cell from the environment until equilibration is achieved (2). If the ψ microbial cell is higher than that of the surrounding environment, the net flow of water will be out of the cell until equilibration is achieved. The latter process probably results in loss of turgor potential first, but if allow to continue, may result in dessication and death of the cell, unless (1) the microorganism can successfully retreat into a dormant spore or other resting body with a wall to slow further water loss or (2), the microorganism can develop a lower osmotic potential (and hence total potential) by osmoregulation (8,27). Osmoregulation (the lowering or raising of the osmotic potential within a cell) is not well understood, but is probably an important mechanism whereby microorganisms maintain turgor and also an equilibrium water potential between their cells and their environment. Osmoregulation is probably an energy-requiring process. Differential abilities in osmoregulation may explain why organisms differ in water

Table 2. Minimum water potentials (−bars) for growth of *Pseudomonas* fluorescens. Estimated from data of Wodzinski and Frazier (3).

	Min water potential (−bars)		
		pH	
°C	5.4	7.0	8.85
15	27	35	21
20	35	42	35
25	42	42	35
30	42	49	42

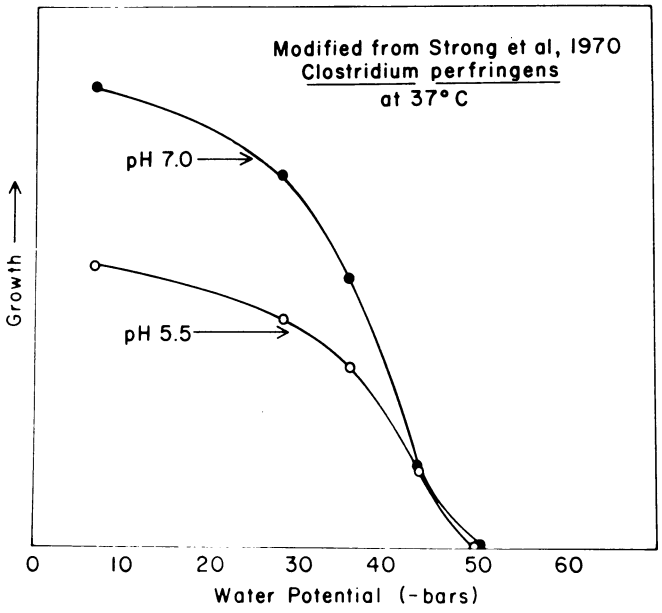

Fig. 2. Relative growth rate of *Clostridium perfringens* in vitro at different water potentials. Estimated from the data of Strong et al. (36).

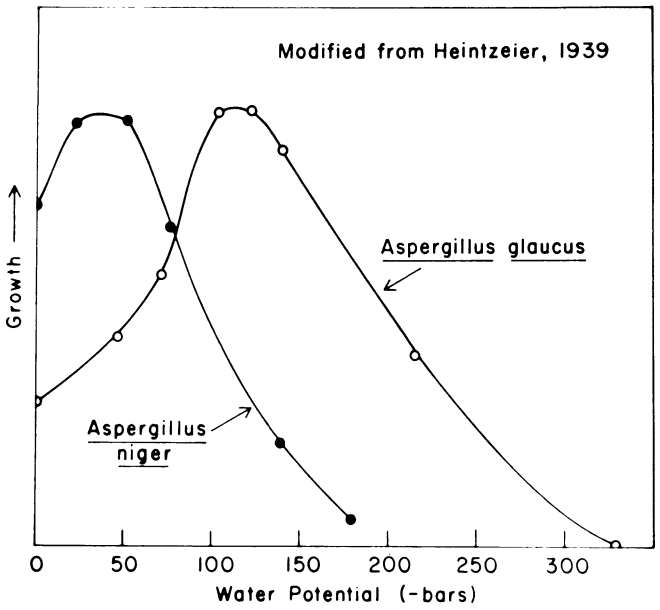

Fig. 4. Relative growth rates of *Aspergillus uiger* and A. *glaucus* at different water potentials. Estimated from the data of Heintzeier (22).

potential requirements according to species, environment, and nutrition.

Thus, the water potential of a microorganism in contact with the surface (skin) of a fruit or vegetable will be in equlibrium with the water potential of the exact site. The water potential of that site, in turn, will probably be somewhere between that of the underlying flesh, and that of the surrounding atmosphere. A microbial cell inside the fruit will be at a water potential in equilibrium with that of the cells (or intercellular spaces) of the fruit. Whether or not growth occurs in any of these sites will be determined by whether the water potential of the site is above the minimum required for growth by the microorganism in question.

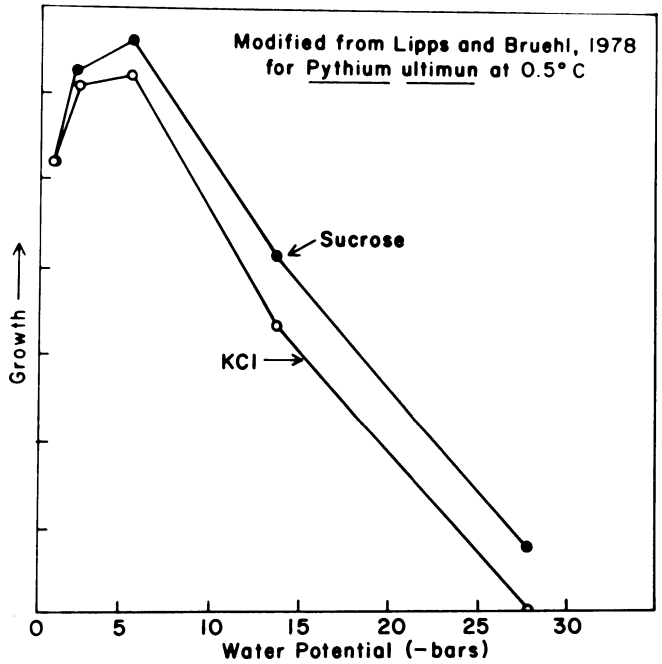

Fig. 3. Relative growth rate of *Pythium ultimum* in vitro at different water potentials. From the data of Lipps and Bruehl (25).

Water potential also plays a role in sporulation and other steps in the life cycles of pathogens. Thus, *Whetzelinia (Sclerotinia sclerotiorum* (Lib.) Korf produces apothecia at near 0 bars but not at -6 bars (21). *Phytophytora cryptogea* and *P. megasperma* release zoospores from sporangia at 0 and −1 mbar soil matric water potential, less so at -10 mbar, and not at all at -25 mbar matric water potential (26). The equilibrium rh at 0, -1, -10, and -25 mbars at 20°C is, respectively, 100, 99.99993, 99.99926, and 99.9981%. The equilibrium Rh for −6 bars is 99.557. Although this range of relative humidities, all above 99.5%, may seem virtually identical to us, they obviously are quite different in terms of response by fungi.

Postharvest water potentials of select fruits and vegetables

Very few data are available to answer the question: What are the water potentials of various fruits and vegetables after harvest or after different periods in storage? We made some measurements and present the results here.

Water potentials were determined for potato tubers (*Solanum tuberosum* L.), peaches and nectarines (*Prunus persica* (L. Batsch,), apricots (*Prunus armeniaca* L.), sweet cherries (*Prunus avium* L.), spur cherries (*P. cerasus* L.), grapes (*Vitis vinifera* L.), blueberries (*Vaccinium angustifolium* Ait.), strawberries (*Frageria Xavanarsa* Duch.) and raspberries (*Rubus strigosus* Michx.). All fruits and the tubers were picked in the summer of 1977 in various locations in Washington State, and the water potentials measured at known times after picking. Exceptions were fruits obtained from a local supermarket; neither the source nor the time of picking was known. Total water potential was determined for individual fruits or tubers with a pressure bomb, where possible. Bomb readings were made with the tubers in the chamber, and by forcing water by pressure out through the cut surface of a short piece of attached stolon preserved intact as part of the tuber at the time of digging. The osmotic potential of expressed juice was determined for the same fruit immediately after making the bomb reading. The juice was absorbed by a disk (2.5mm diam) of Whatman No.1 ^{3} filter paper and placed in a sample changer psychrometer. Some readings were repeated for sap from tissues frozen in liquid nitrogen to destroy cell membranes, then warmed to room temperature. Readings were also made at different times after picking to evaluate the influence of storage time on water potential of a fruit or tuber.

Potato tubers had the highest water potential of all tissues tested (Table 3). Readings of water potential by pressure bomb were possible only on tubers tested less than 24 hr after digging. The values were between −6 and −7 bars. The stolons were brittle and unsuitable for

Table 3. Water potentials of potato tubers and certain fruits.

Fruit or tuber	Location in Washington where grown	Time after harvest (hr)	ψ (bomb)[z] (−bars)	π Freezing[y] before (−bars)	π Freezing[y] after (−bars)
Russett Burbank	Lind	24	6.5±1.6	6.4±0.7	8.4±0.05
Potato tubers	Pullman	24		7.5±0.64	9.0±0
Strawberries	Puyallup	4	11.1±2.1	10.2±1.9	
		24	11.7±1.7	10.2±0.9	
		48	17.4±5.7	13.4±1.3	
Raspberries	Pullman	4	11.4±1.8	14.2±1.1	
	Puyallup	1		12.3±1.2	
		4	11.5±1.5	12.7±0.3	
		48	17.1±2.7	13.6±2.0	
Raspberry juice					11.9±1.0
Peaches	Pullman	1		15.2±3.8	
		65	17.4±2.5	12.8±1.1	
	Clarkston	4	14.0±2.6.	10.5±0.6	
		96	16.3±2.3	11.9±0.4	
		168	11.2±1.3	10.3±1.1	
Nectarines	Purchased[x]			16.2±4.3	
Apricots	Pullman	2	18.9±1.4	13.2±3.4	
		65	19.7±2.2	15.5±3.5	
	Purchased[x]			12.5±0.8	
Seedless grapes	Purchased[x]		7.7±0	28.5±1.2	
Blueberries	Puyallup	5	14.8±0.3	17.1±2.2	
		48		17.8±0.7	
Sweet Cherries	Mt. Vernon	6	25.1±1.0	24.6±2.8	
		20	31.6±2.9	29.0±1.3	
		30	23.0±1.2	27.0±4.9	
	Royal Slope	44		38.3±1.5	
	Purchased[x]			46.9±5.0	

[z]ψ = total water potential measured by pressure bomb.

[y]π = osmotic potential measured by psychrometry.

[x]Purchased from Pullman supermarket.

bomb readings after several days in the lab. The osmotic potential of fresh sap was also between −6 and −7 bars (about 1 bar lower for 10-day-old tubers). When the tubers were frozen in liquid N, thawed, and read, osmotic potentials of -8.5 to -9.0 bars were obtained. These values probably approximate the osmotic potential of intact cells. This indicates that the tubers had about 1 to 2 bars of tugor potential. Radtke (32) obtained similar values for the osmotic pressure of frozen/thawed tuber slices at 8-9 atm (≃-8 to -9 bars water potential) and A. Kelman, Univ. Wisconsin, Madison, (personal communication) likewise has found tubers to have osmotic potentials of −8.3 to -9.4 bars plus 0.8 to 1.4 bars turgor or total potential of -7.0 to -8.5 bars.

The water potentials and juice osmotic potentials of the various fruits tested are given in Table 3 and summarized in Fig. 5. In general, strawberries had the highest water potentials at -10 to -14 bars; peaches, nectarines, and apricots ranged between -10 and -16 bars; raspberries ranged between -12 and -15 bars; blueberries were -15 to -17 bars; and sweet cherries ranged between -25 and -50 bars. With the exception of grapes and sour cherries, none of the fruits had more than 1 to 2 bars turgor potential, and most measurements indicated no turgor potential. As with potato tubers, we found the bomb readings impossible or unreliable with fruit held in storage for more than a few days, or even a few hours. Readings of stored fruit by the bomb method were higher (water potential lower) than for juice of the same fruit read with the psychrometer, suggesting the existence of a negative turgor potential. We believe this is an artifact, possibly caused by gums or other materials formed in the stem of the fruit after picking and thereby responsible for a high resistance to extrusion of water through the stem when air pressure was applied to the fruit. Bomb readings made within 4 to 6 hr after picking were generally close to the osmotic potential reading, indicating low turgor pressure of the fresh fruit.

Ripe sour cherries were picked at Pullman and read for both the total and osmotic potentials following different periods of storage at 4°C. Within 1 hr of picking, total water potential was about -15 bars, and the juice osmotic potential was about -30 bars (Fig. 6). Readings of osmotic potential before and after freezing were similar. By calculation from eq. 2, the turgor potential of the cherries at picking was about 15 bars. Following storage, the osmotic potential did not change, but the total potential decreased (became more negative) until the two values were the same 144 hr after picking (Fig. 6). Apparently, cell turgor was lost during storage and was virtually nil after 144 hr.

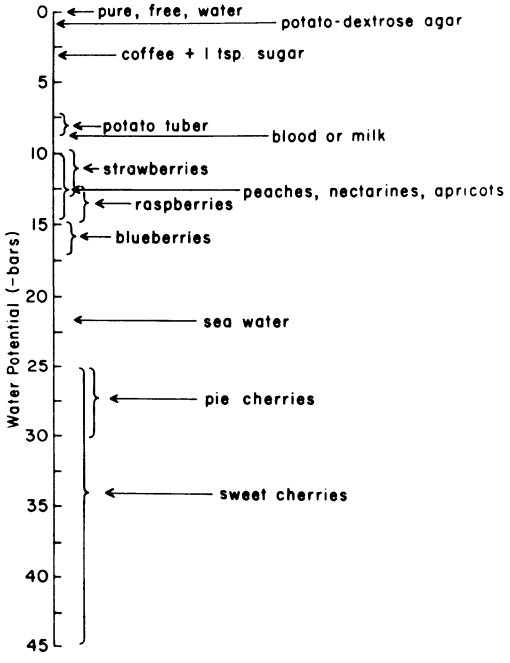

Fig. 5. Summary diagram of the water potentials of some common substances and the potato tubers and various fruits.

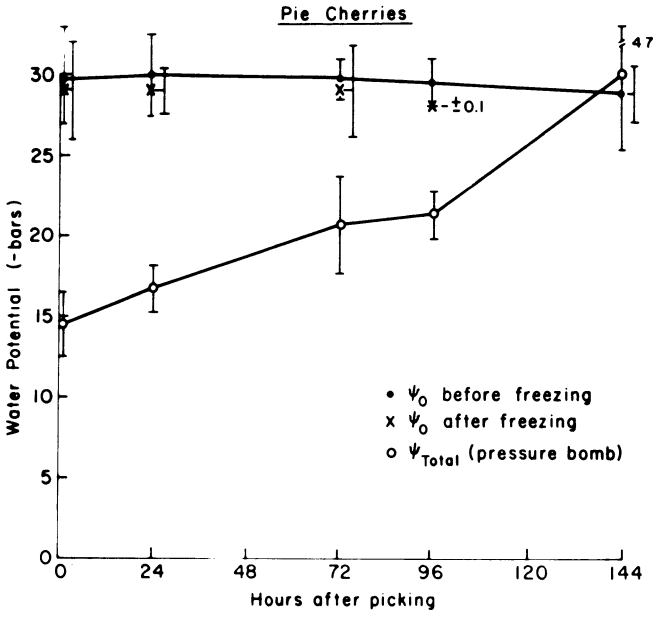

Fig. 6. Water potential of sour (pie) cherries at different times after picking.

Microoganisms must obtain their water by having a water potential lower than the total water potential of their environment or otherwise expending energy. Thus, a hypothetical organism in one of the pie cherries used in our experiment would need a ψ microbial cell lower than only -15 bars at the time of picking to obtain water from the cherry, but lower than -30 bars after 6 days in storage to obtain the same water for growth.

Another study was conducted to determine whether the variation in osmotic potentials of fruit sap was due to variations in sugar content. The Brix (31) method was used to obtain a value for amount of solutes (mainly sugars) in sweet cherries, fresh raspberries, raspberry juice (frozen and thawed), and fresh strawberries. The same fruit used for the Brix reading was used to obtain juice for determination of the osmotic potential. The correlation between the two was highly significant at r = 0.98 (Fig. 7). Apparently, the variation in osmotic potentials of the juice of fruits (e.g., sweet cherries) is due to variations in sugar content. With these measurements, the Brix reading can be converted to osmotic potential (π) by the relationship, π = 7.79 - 2.14 Brix.

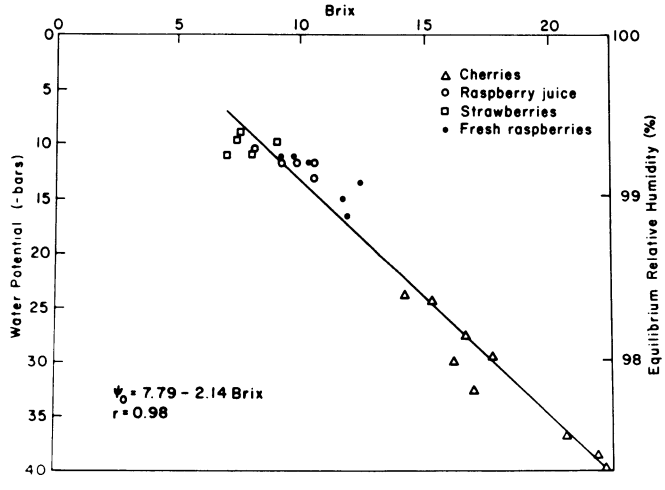

Fig. 7. Relationship of percentage solids (Brix reading) and water potential as determined by psychrometry reading of the juices of certain fruits.

Water potential and the development of plant disease

Production of the plant disease is a complex process that results from an interaction between the host and pathogen and includes production of toxins or degrading enzymes by the pathogen, and defense reactions of the host. The role of water potential in these various disease processes is virtually unknown. There is good evidence with certain root diseases that the stress associated with low plant water potentials results in more severe disease (10,29). However, the exact mechanisms by which such stress favors disease (e.g.: does the low water potential slow the defense reaction of the host, increase pathogenicity of the pathogen, or both?) is unknown. Most work on the physiology of the hostpathogen interaction is done without regard to water potential. This section is thus restricted mainly to the more elementary considerations of whether some host tissues (e.g., fruit or vegetable tissues) have a water potential too low for a potential pathogen.

In an earlier review (14), we called attention to an apparent correlation between water potential requirements for growth of a pathogen *in vitro* and production of root diseases by that pathogen *in vivo*. Thus, fungi with ability to grow at low water potentials, e.g., *Fusarium* species (11), cause the greatest amount of disease under dry soil conditions, and those that grow best at relatively high water potentials, e.g., *Pythium* and *Phytophthora* species, cause the greatest amount of disease in wet soil. *Gaeumannomyces graminis* (Sacc.) Arx and Olivier var. *tritici* Walker, cause of wheat (*Triticum aestivum* L.) take-all, cannot grow at water potentials below -40 to -45 bars, and its growth rate is reduced by half at about -20 bars. Wheat under dryland conditions develops plant water potentials of -30 to -40 bars, and some plants near Pullman were recorded at -50 bars at heading during the drought of 1977. Take-all occurs mainly with wet-soil conditions and the most logical reason is that the host water potentials are unsuitable for growth of the pathogen under severe dryland conditions.

The water potentials of fruits and tubers (-10 to -50 bars) clearly are ideal for microbial growth. Potato tubers especially should be ideal for growth of bacteria. It is thus not surprising that 5 or 6 bacterial diseases are known to affect potato tubers (3), including ring rot [*Corynebacterium spedoicum* (Spieck. & Kotth.) Skapt. and Burkh.], soft rot [*Erwinia carotovora* var. *carotovora* (Jones) Dye], blackleg and associated tuber rot [*E. cartovora* var. *atroseptica* (van Hall) Dye], and various secondary tuber rots and seedpiece rots. In contrast, sweet cherries, with sufficient sugar to produce a water potential approaching -50 bars, will very likely limit the growth of bacteria. Bacterial fruit rots of cherries are apparently rare or unknown (3), as are many fungal rots of cherries. On the other hand, there are many fruit-decay problems of peaches (-10 to -15 bars) caused by fungi, including *Botrytis cinerea* Pers. ex Fr., *Monilinia fructicola* (Wint.) Honey and *M. laxa* (Aderh. and Ruhl.) Honey, *Rhixopus stonlonifera* (Ehr. ex Fr.) Lind, and others (3). The main causes of fruit decay of strawberries are also fungi (*B. cinerea* and *R. nigricans*) but soft rot caused by *E. cartovora* var. *carotovora* also affects strawberries (3).

Direct evidence is lacking to say that water potential determines which pathogens will cause damage in a particular fruit or vegetable. Nevertheless, it seems likely that a water potential limiting to growth of a bacterium or fungus on agar media will also be as limiting, if not more so, to that bacterium or fungus on or in plant tissues in nature. Nutrient agar media are energy-rich and usually all other conditions, e.g., pH and temperature, are ideal for the test organism. An accurate assessment of the growth capability of an organism at different host water potentials should be made by growing the test organism in the host tissue. An equally important question is whether water potentials limiting to growth will also limit production of enzymes, toxins or other agents of pathogenesis. For antibiotic production, Bruehl et al. (17) found for *Cephalosporium gramineum* Nisikado & Itaka that greatest antibiotic production for a given amount of mycelial growth occurred at the lower limits of water potential needed for growth. No antibiotic production occurred in the absence of growth. Antibiotic production and toxin production probably are similar microbial processes. It is also likely in some cases that production of enzymes or toxins necessary to produce disease symptoms will cease at water potentials above those limiting to growth of the pathogen itself. In such cases, the tissue need not be at a water potential sufficiently low to stop growth of the pathogen completely, only low enough to slow or stop pathogenesis.

Another important water parameter in the development of diseases in storage is the films of water that may form on the surfaces of fruits and vegetables from condensation. The water potential of such films is probably near 0, except for whatever osmotic component may exist due to leakage of nutrients from or through the skin into the film. Such water films function as a barrier to gas exchange between the fruit and the surrounding atmosphere. With potato tubers, a thin water film helps increase tuber soft rot caused by *Erwina carotovora* var. *carotovora,* due to the anaerobic conditions maintained at the tuber surface (30). Water films are also excellent habitats for saprophytic bacteria, some of which may be antagonistic to pathogens. Considerably more work is needed to unravel the indirect as well as direct effects of water on plant disease, including postharvest plant diseases. Such work should be forthcoming much more rapidly now that the water potential concept is in use, and now that methods are available to measure water potential.

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