Plant Hydraulic Structure and Function

1. Central Role in Plant Function

2. Water Potential

3. Water in plant cells

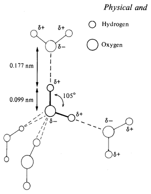
4. Transport of water
-Soil to root
-Root to leaf

5. Water Limitations and Plant Responses

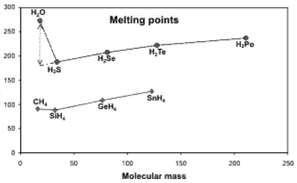
6. Measurement techniques

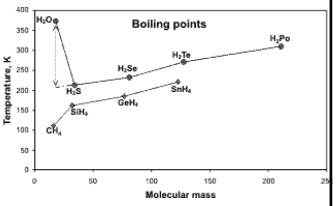
Water has wide ranging importance in plant function

-Structural supporter (e.g. cell turgor)
-Structural constituent (e.g. protoplasm)
-Acquirer/transporter of materials
-Solvent
-Reactant
-Temperature regulator



Anomalous properties of water – due to strong dipole moment/H bonding





1.Water has unusually high melting point. [explanation]
2.Water has unusually high boiling point. [explanation]
3.Water has unusually high critical point. [explanation]
4.Water has unusually high surface tension and can bounce. [explanation]
5.Water has unusually high viscosity. [explanation]
6.Water has unusually high heat of vaporization. [explanation]
7.Water shrinks on melting. [explanation]
8.Water has a high density that increases on heating (up to 3.984°C). [explanation]
9.The number of nearest neighbors increases on melting. [explanation]
10.The number of nearest neighbors increases with temperature. [explanation]
11.Pressure reduces its melting point (13.35 MPa gives a melting point of -1°C) [explanation]
12.Pressure reduces the temperature of maximum density. [explanation]
13.D_2O and T_2O differ from H_2O in their physical properties much more than might be expected from their increased mass; *e.g.* they have increasing temperatures of maximum density (11.185°C and 13.4°C respectively). [explanation]
14.Water shows an unusually large viscosity increase but diffusion decrease as the temperature is lowered. [explanation]
15.Water's viscosity decreases with pressure (at temperatures below 33°C). [explanation]
16.Water has unusually low compressibility. [explanation]
17.The compressibility drops as temperature increases down to a minimum at about 46.5°C. Below this temperature, water is easier to compress as the temperature is lowered. [explanation]
18.Water has a low coefficient of expansion (thermal expansivity). [explanation]
19.Water's thermal expansivity reduces increasingly (becoming negative) at low temperatures. [explanation]
20.The speed of sound increases with temperature (up to a maximum at 73°C). [explanation]
21.Water has over twice the specific heat capacity of ice or steam. [explanation]
22.The specific heat capacity (C_P and C_V) is unusually high. [explanation]
23.Specific heat capacity; C_P has a minimum. [explanation]
24.NMR spin-lattice relaxation time is very small at low temperatures. [explanation]
25.Solutes have varying effects on properties such as density and viscosity. [explanation]
26.None of its solutions even approach thermodynamic ideality; even D_2O in H_2O is not ideal. [explanation]
27.X-ray diffraction shows an unusually detailed structure. [explanation]
28.Supercooled water has two phases and a second critical point at about -91°C. [explanation]
29.Liquid water may be supercooled, in tiny droplets, down to about -70°C. It may also be produced from glassy amorphous ice between -123°C and - 149°C [74] and may coexist with cubic ice up to -63°C [137]. [explanation]
30.Solid water exists in a wider variety of stable (and metastable) crystal and amorphous structures than other materials. [explanation]
31.Hot water may freeze faster than cold water; the Mpemba effect. [explanation]
32.The refractive index of water has a maximum value at just below 0°C. [explanation]
33.The solubilities of non-polar gases in water decrease with temperature to a minimum and then rise. [explanation]
34.At low temperatures, the self-diffusion of water increases as the density and pressure increase. [explanation]
35.The thermal conductivity of water is high and rises to a maximum at about 130°C. [explanation]
36.Proton and hydroxide ion mobilities are anomalously fast in an electric field [explanation]
37.The heat of fusion of water with temperature exhibits a maximum at -17°C [15]. [explanation]
38.The dielectric constant is high and behaves anomalously with temperature. [explanation]
39.Under high pressure water molecules move further away from each other with increasing pressure. [explanation]
40.The electrical conductivity of water rises to a maximum at about 230°C and then falls. [explanation]
41.Warm water vibrates longer than cold water. [explanation

Anomalous properties of water

-In trees can be both superheated and supercooled

-Fun experiments with water

-polywater

In the Correspondence section of the October 11, 1969 issue of Nature, the following letter appeared under the heading, "Anomalous" Water:

SIR,—A report on the properties of "anomalous" water appeared recently in Nature (222, 159; 1969). The probable structure of this phase was reported by Lippincott et al.1 who refer to the phase as polywater, a terse descriptive of the structure.

The properties of polywater are negligible vapour pressure, density ~1.4 g/cm3, partial miscibility with normal water (depending on the length of the polymer chains) and stability to temperatures ~500ºC. The polymer chains are some 250-420 kJ/mole (60-100 kcal/mole) of monomer more tightly bound than normal water.

I need not spell out in detail the consequences if the polymer phase can grow at the expense of normal water under any conditions found in the environment. Polywater may or may not be the secret of Venus's missing water. The polymerization of Earth's water would turn her into a reasonable facsimile of Venus.

There are examples of phases in other systems which are difficult to nucleate. Once the nuclei are present, the phases grow readily, often by mechanisms other than those required to form the nuclei. It is almost a truism that, under conditions where both a stable phase and a metastable phase may form, the metastable phase forms first. In this case the metastable phase would be normal water.

After being convinced of the existence of polywater, I am not easily persuaded that it is not dangerous. The consequences of being wrong about this matter are so serious that only positive evidence that there is no danger would be acceptable. Only the existence of natural (ambient) mechanisms which depolymerize the material would prove its safety. Until such mechanisms are known to exist, I regard the polymer as the most dangerous material on earth.

Every effort must be made to establish the absolute safety of the material before it is commercially produced. Once the polymer nuclei become dispersed in the soil it will be too late to do anything. Even as I write there are undoubtedly scores of groups preparing polywater.

Scientists everywhere must be alerted to the need for extreme caution in the disposal of polywater. Treat it as the most deadly virus until its safety is established.

Yours faithfully,

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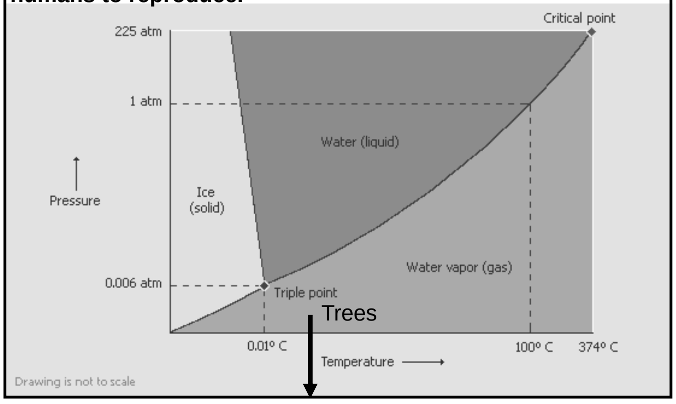
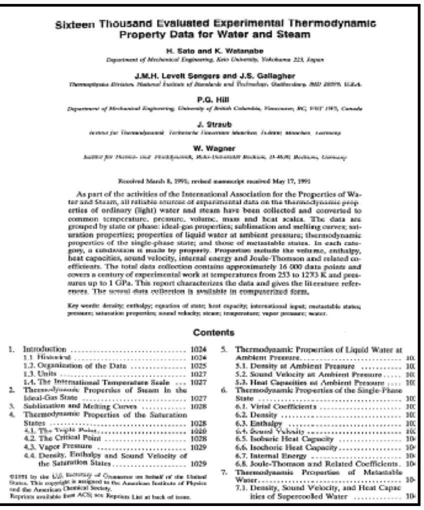
Water is in a very peculiar state in trees: a metastable liquid under 'negative pressure' (tension) Cohesion/adhesion stabilizes the liquid water, and in a way that is very hard for humans to reproduce.



J. Phys chem. V20 1991



Sixteen Thousand Evaluated Experimental Thermodynamic Property Data for Water and Steam

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As part of the activities of the International Association for the Properties of Water and Steam, all reliable sources of experimental data on the thermodynamic properties of ordinary (light) water and steam have been collected and converted to common temperature, pressure, volume, mass and heat scales. The data are grouped by state or phase: ideal-gas properties; sublimation and melting curves; saturation properties; properties of liquid water at ambient pressure; thermodynamic properties of the single-phase state; and those of metastable states. In each category, a subdivision is made by property. Properties include the volume, enthalpy, heat capacities, sound velocity, internal energy and Joule-Thomson and related coefficients. The total data collection contains approximately 16 000 data points and covers a century of experimental work at temperatures from 253 to 1273 K and pressures up to 1 GPa. This report characterizes the data and gives the literature references. The actual data collection is available in computerized form.

Key words: density; enthalpy; equation of state; heat capacity; international input; metastable states; pressure; saturation properties; sound velocity; steam; temperature; vapor pressure; water.

Contents

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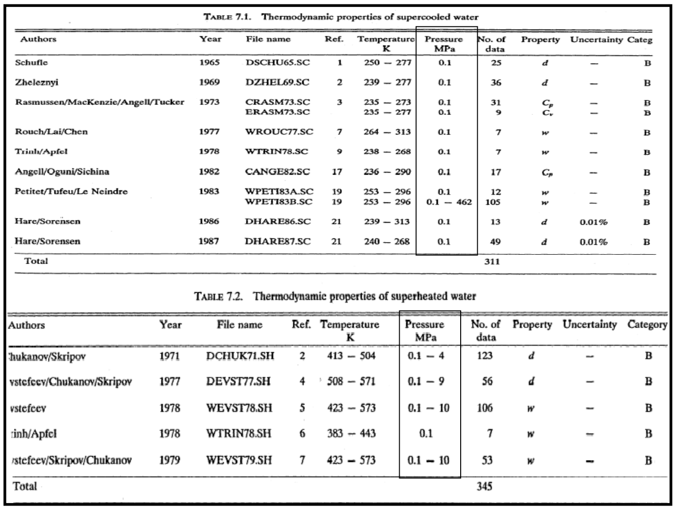


TABLE 7.1. Thermodynamic properties of supercooled water

Authors	Year	File name	Ref.	Temperature K	Pressure MPa	No. of data	Property	Uncertainty	Categ
Schufle	1965	DSCHU65.SC	1	250 – 277	0.1	25	*d*	–	B
Zheleznyi	1969	DZHEL69.SC	2	239 – 277	0.1	36	*d*	–	B
Rasmussen/MacKenzie/Angell/Tucker	1973	CRASM73.SC	3	235 – 273	0.1	31	C_p	–	B
		ERASM73.SC		235 – 277	0.1	9	C_v	–	B
Rouch/Lai/Chen	1977	WROUC77.SC	7	264 – 313	0.1	7	*w*	–	B
Trinh/Apfel	1978	WTRIN78.SC	9	238 – 268	0.1	7	*w*	–	B
Angell/Oguni/Sichina	1982	CANGE82.SC	17	236 – 290	0.1	17	C_p	–	B
Petitet/Tufeu/Le Neindre	1983	WPETI83A.SC	19	253 – 296	0.1	12	*w*	–	B
		WPETI83B.SC	19	253 – 296	0.1 – 462	105	*w*	–	B
Hare/Sorensen	1986	DHARE86.SC	21	239 – 313	0.1	13	*d*	0.01%	B
Hare/Sorensen	1987	DHARE87.SC	21	240 – 268	0.1	49	*d*	0.01%	B
Total						311			

TABLE 7.2. Thermodynamic properties of superheated water

Authors	Year	File name	Ref.	Temperature K	Pressure MPa	No. of data	Property	Uncertainty	Category
hukanov/Skripov	1971	DCHUK71.SH	2	413 – 504	0.1 – 4	123	*d*	–	B
vstefeev/Chukanov/Skripov	1977	DEVST77.SH	4	508 – 571	0.1 – 9	56	*d*	–	B
vstefeev	1978	WEVST78.SH	5	423 – 573	0.1 – 10	106	*w*	–	B
inh/Apfel	1978	WTRIN78.SH	6	383 – 443	0.1	7	*w*	–	B
stefeev/Skripov/Chukanov	1979	WEVST79.SH	7	423 – 573	0.1 – 10	53	*w*	–	B
Total						345			

To understand the multifarious role of water in plant function, we must consider both the *states* of water, and *rates* of movement of water in plants.

Both states and rates are determined by values of, or gradients in, water potential (Ψ).

Water Potential: The free energy, embodied in water, available to perform work.

Units: Energy density (J/m^3), or pressure (Pa = N/m^2)

Values: Pure, free water, at STP = O MPa (call this Ψ_o)
Water with solutes at STP always < 0 MPa
Pure water under perfect vacuum, ST = -0.1 MPa
Water in stressed leaves ~ up to –2.5 MPa

That’s right: 25 times more ‘powerful’ than atmospheric pressure! (but ‘pulling’ rather than ‘pushing’)

Speaking of “pulling” rather than “pushing”…

- **Water anywhere in plants (and soils for that matter) is almost always at a value of Ψ that is <0. (If you’re thinking of turgid leaves – they are also at Ψ <0 !!)**

- **That is why we’ll almost always see (-) signs in front of Ψ values.**

- **Because water flows down a gradient in water potential, this means that leaves must have more negative values of Ψ than soil or roots, to drive flow.**

- **In other words, water is ‘pulled’ under tension through plants rather than ‘pushed’.**

- **There are some serious challenges to accomplish this!**

Water Potential in any location in a plant is a summation of several possible contributing variables.

- •Hydrostatic Pressure (e.g. elastic cell walls, root pressure)
- •Gravity (tall trees!)
- •Solute concentration (‘osmotic potential’)
- •Matric potential (electrostatic interactions with porous media – soil pores, cell surfaces)

$$\Psi_{total} = \Psi_p + \Psi_g + \Psi_s + \Psi_m$$

Let’s take a look at each of these components…

Water potential due to gravity.

$\Psi(h)$ = simply, the potential energy associated With moving water to height, h

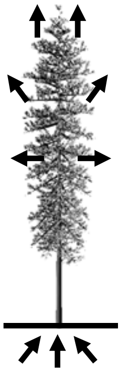
$\Psi(h)$ = mass x acceleration due to gravity x h

Since this has energy units of Joules, to obtain pressure units, we can use the density of water instead of mass.

$\Psi(h) = \rho gh = (1000\ kg/m^3) x (9.8\ m/s^2) \times h\ (m)$

OR, simply, $\Psi(h)/h = 0.01$ MPa / m

Water potential due to gravity (cont.)



Thus, water in leaves at the top of a 100m tall tree must ‘suck’ water with -10 x atmospheric pressure (-1 MPa) – and that is just to maintain the water there.

To move water through the frictional pipes of the woody vascular tissue requires even more of a ‘pull’.

Might this be a factor regulating maximum tree height?

Water potential due to solutes.

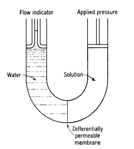
There are 2 tangible pieces of evidence that can convince us that solutes lower Ψ below that of Ψ_o

1. If an aqueous solution is put into contact with pure water via a semi-permeable membrane, it will suck water in.

2. The vapor pressure of water overlying an aqueous solution (in equilibrium) will always be less than that of the vapor pressure of pure water (at the same temperature). The solution ‘holds onto’ water in the liquid state more than the pure water. (e.g. seawater/freshwater @ 50^{O}F =.167 / .178 lb/in^2)

Water potential due to solutes (cont.)

Ψ_s can be experimentally measured simply as the amount of pressure needed to prevent water from moving from the solution to the pure water.



Ψ_s is calculated simply as:

$$\Psi_s = RT \ln (N_w)$$

where R is the gas constant
T is temperature
N_w is mole fraction of h2o

Since $N_w < 1$, $\ln(N_w) < 0$

Water potential due to solutes (cont.)

We can start to think about how plants/cells might take advantage of this.

A 1 Molar solution = -2.4 MPa = a water column 240 m tall!! (and this value is not unheard of in plant cells). (e.g. 180 g sugar in 1 L water = 1M)

"Osmotic regulation" is a term describing cellular loading of solutes in order to bring water in when its hard to acquire. (But there are costs of too much solute…)

Water potential due to hydrostatic pressure

This is perhaps the easiest component of Ψ to understand – it is simply the mechanical pressure exerted on water (in excess of atmospheric).

E.g. if you push on a water balloon (or the walls of an already turgid balloon push on the water within), you are conferring x MPa of Ψ_p to the water within it.

Ψ_p is simple Force/Area – the way we usually think of pressure; e.g. $1\ N/m_2 = 1\ Pa$

Water potential due to hydrostatic pressure

Roots in some species can generate mild positive pressures.

Leaf cells can maintain positive turgor pressures even when the water around them is at very (-) water potentials – How can this be?

To see, let's forget about gravity and matric for now:

$\Psi_{total} = \Psi_s + \Psi_p$
An example could be –2.5 MPa = -2.8 MPa + 0.3 MPa
i.e. Ψ_{total} only depends on the sum of components!

Water potential due to matric forces

Water adheres electrostatically to solid surfaces (soil particles, interior of cell walls). These surfaces are generally hydrophilic (lots of OH groups hanging on the surface). Water is thus attracted to many porous media, generating Ψ_m.

Air/water menisci in porous media also create large surface tensions that draw water in.

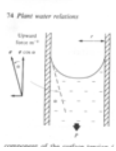
A hydrophobic porous media would confer a +, rather than (-) Ψ_m, but this doesn't really happen in soil/plant systems.

Matric potential in tiny intercellular spaces in leaves (menisci) generates the pull on the water column that drives the ascent of sap!

Water potential due to matric forces (cont.)

Capillary rise is associated with matric potential.

Lifting force = circumference x Surface Tension
$2\Pi r$ x .073 N/m (r is pore radius)



Downward force = height x area x density x g
h x $2\Pi r^2$ x 1000 kg/m^3 x 9.81

Solving for h

h = 1.5 x 10-5 m^{-2} / r (in meters)

Examples: capillary radius = 1 um, h = 1.5 m
= 75 um, h = .02 m (typical for plants)
This means that water cannot rise in trees by capillarity!

Water potential due to matric forces (cont.)

Instead of a force balance, we can express the previous equations in terms of pressure balance (Force/Area), which gives an expression for the pressure needed to drain a pore space (soil or plant)

Pressure (MPa) ~ 0.3/diameter(um)

Soils/plants with a wide distribution of pore sizes 'give up' their water more evenly with drying!

Water potential – conclusions

The concept of water potential unifies gravitational, solute, matric, and pressure forces acting within plants.

Plants primarily have solute potential under direct physiological control, in order to affect needed values of pressure potential, or overcome matric/gravitational potential.