BOT 4503
5 hours
Water Potential including biologically relevant properties of water
(Plus appendices)

Objectives

1. Briefly, who was J. Willard Gibbs? . . .Stephen Hales?

2. Describe three types of water movement.

3. Calculate the effect of gravity on a water column (i.e., be able to recreate the logic shown in the overhead entitled "Hydrostatic pressure . . ."). Name conditions in which hydrostatic pressure that results from gravity will be important. Express atmospheric pressure in as many ways as you can.

4. What is the formal definition of diffusion? What is chemical potential? (Your answer to this last should include examples of aqueous solutions the water of which have different chemical potentials.)

5. Quantitatively discuss the three parameters that affect diffusion. Relate your discussion to questions of diffusion in plants.

6. Describe factors that affect the movement of water. What is a matrix effect? When might it be biologically relevant to consider?

7. What is vapor pressure? . . . partial pressure? What is the driving force for gaseous water movement?

8. What are colligative properties of water? How do they depend on the nature (e.g., large, small, charged, polar, &c) of the solute, ideally? Name the colligative properties. Know the forms of the equations and be able to predict quantitatively the effect of addition of X solute to Y water. (Commit to memory the quantitative effects of addition of a solute to water.) Define molar, molal, mole fraction.

9. Draw an osmometer. Go through several iterations of dropping the bulb containing X solution into a bathing solution, and predict the rise in the water column.

10. Why are relative water content and tissue water content inadequate expressions of the water status of a plant? Describe contexts in which these terms may be usefully applied.

11. Define in a rigorous way water potential. What are the units? What is the reference state? What are the components?

12. Can the concept of water potential be used to predict bulk flow? If not, describe how it might fail with the use of the osmometer. (Hint: what happens if you puncture the bulb?) Then, give a real plant example that demonstrates that with bulk flow, water does NOT move from a region of high water potential to a region of low water potential.

13. Can the concept of water potential be used quantitatively to assess the driving force for the diffusion of gaseous water? If not, what is the driving force for gaseous water diffusion?

14. Give typical values for the water potential of leaves. What are the magnitudes of the components of water potential in a leaf?

15. The previous question addressed average values, but the components of water potential vary from one cell type to another. Elaborate and give examples.

16. Give typical values for water potentials in the soil-plant continuum for a transpiring plant.

17. What is the largest driving force for water loss from the plant?

18. How do root hairs facilitate water uptake from the soil? Describe water movement at the soil-plant interface.

19. Draw a cross-section of the root. Identify the endodermis. Draw a 3-D representation of the endodermis and label the casparian strips. What is the role of the endodermis in water uptake? Do roots offer resistance to water uptake? . . . example experiment? Are roots necessary for transpiration?

20. What is the exodermis?

21. Describe water movement from the root hair to the xylem.

22. Describe how root pressure can be generated by analogy with the osmometer.

23. What is capillarity? Can it account for the ascent of sap in tall plants?

24. Is root pressure a naturally occurring phenomenon? If so, what are the magnitudes? What is guttation? Give examples of plants that exhibit this phenomenon. Are the contents of the xylem always under negative pressure? Can root pressure be used as a universal explanation for the ascent of sap? If no, why not?

25. Can barometric pressure account for the ascent of sap? If no, why not?

26. Do plants have fluid pumps?

27. What is the cohesion theory of sap ascent? How can you demonstrate that xylem sap is under tension? How does the tensile strength of water match the requisite tensions?

28. Describe the different types of tracheary elements? Which offers less resistance to water flow? . . . why? What is cavitation? Which type of tracheary element is most susceptible? How can cavitation be reversed, or how are the effects limited?

29. What is peristomatal evaporation?

30. Describe the principle of psychometry. How could you use this principle to measure the water potential, the solute potential, and the pressure potential?

31. What is a pressure bomb? Describe its use to measure water potential.

32. What is the pressure probe?

33. Describe some effects of water insufficiency on plants. Name some sensitive processes that stop when the water potential is shifted more negative.

34. Briefly, identify some mechanisms on plants use in response to water insufficiency.

35. What are water channels (aquaporins)?

Lecture

This unit on the water status of plants will be broken into two major parts. First, we will organize our thoughts about water in general, and second, we will focus on how water moves in a plant and how we can measure the changes in water status and relate them to physiology. These categories are obviously somewhat arbitrary, and, of course, we will relate the categories one to another. I think you have some surprises in store! Thermodynamics—the first part—is an old science. You would, therefore, properly assume that we “understand” water, the so-called universal solvent. Not to mention, whilst showing a hint of nationalism, that thermodynamics is as American as apple pie—indeed, it was J. Willard Gibbs, the American mathematician and physicist born in 1839, who thought through such problems, and was perhaps the American who attracted attention to our scientific potential. Water transport in plants, &c.—the second part—is also an old science. At least as far back as the 1600's, scientists were conducting experiments on transpiration. (These experiments were rather simple, e.g., measurements of weight loss of potted plants.) As a point of interest, Stephen Hales (1677-1761)—the father of plant physiology—was a water-relations man.

A first step is to organize what we know about water in general. We may say that water movement can be broadly divided into three types:

(1) bulk flow—this is the simplest form of water movement, and it results from a hydrostatic pressure difference. When you turn a spigot handle, water flows in bulk from the orifice because the pressure there is less than the pressure in the connecting tube. The hydrostatic pressure wherever may be a constant, or it may vary in some predictable way. Consider the effect of gravity.

Overhead 1: Gravitational contributions to hydrostatic pressure

A tall vertical column of water—e.g., in the xylem of a 100-m redwood tree—will exert a lot of pressure at the base of the tree simply because of the mass of the column. It is a rather straightforward matter to calculate the magnitude of this pressure, and it is easy to match this calculation with your own experiential base. Consider a cubic centimeter (cc) of water, which has a volume of 1 ml and a nominal mass of 1 gram (=10^{-3} kg). At the base of the cubic centimeter, the force (F) exerted is 10^{-3} kg (mass) x 10 $\mathrm{m \cdot s^{-2}}$ (acceleration of gravity). This force is distributed over 1 $\mathrm{cm^2}$ (=10^{-4} $\mathrm{m^2}$), so the pressure (P) is given by F/A or (10^{-3} kg x 10 $\mathrm{m \cdot s\text{-}^{2}}$)/($10^{-4}$ $\mathrm{m^2}$) or 10^2 ($\mathrm{kg \cdot m \cdot s^{-2}}$)/$\mathrm{m^{-2}}$. This latter simplifies to 10^2 $\mathrm{N \cdot m^{-2}}$. (A Newton is the derived SI unit for force, and is $\mathrm{kg \cdot m \cdot s^{-2}}$.) The SI unit for pressure is the Pascal (=N · m^{-2}), so a column of water one centimeter tall will exert a pressure of 10^2 Pa. A column of water one-meter high will have a pressure of 10^4 Pa at the base, which is equal to about 0.1 atmospheres. At the expense of redundancy, then ,10^5 Pa = 100 kPa = 0.1 MPa = 1 atm = 1 bar = 14.7 psi = 76 cm Hg or 30 inches Hg = 10 m H_20 or 31 feet H_2O. The conclusion that can be drawn from these figures is: over short vertical distances, gravity is relatively unimportant because, as I mentioned previously, the pressures in plant cells are on the order of atmospheres. Gravity is important in tall plants, such as the redwood that I alluded to, and gravity is important in the movement of soil water. Hydrostatic pressure differences in general, but not attributed to gravity, are always important.

Overhead 2: Diffusion considerations

(2) Diffusion, defined formally, is the migration of a substance under the action of a difference in the chemical potential. (Said another way, diffusion is a spontaneous process (i.e., thermodynamically associated with a loss of free energy) leading to the net movement of a substance from one place to another.) In bulk flow, there is a relationship between the positions of two molecules over time. I.e., if you open a hose bibcock, water flows out, and the water molecules that flow out together were seconds earlier also together in the plumbing tubing. In diffusion, there is no relationship between two molecules over time; diffusion is a statistical process—diffusion is the net movement of molecules, but during that net movement, some molecules may have moved from one region to the other, whereas a different molecule may have moved *vice versa*. For a system consisting of only one substance and being constant and homogeneous in all parameters except the number of molecules of that substance, the chemical potential is related to the number of molecules in one area of the system, which may be compared to the number of molecules in another area of the system. That is a mouthful, so we make the somewhat accurate statement—valid only for diffusion of uncharged entities—that "a substance moves from a region of its high concentration to a region of its low concentration." As you know, water molecules—liquid or gaseous—are in constant movement because of their thermal energy. Water molecules move in all directions until the system is at the lowest free energy (i.e., until the "concentration" of this pure water is the same throughout the system). As an example, if we ignore isotope effects, and place a liquid droplet of ^{16}O-water in the middle of a container of ^{18}O-water at the same temperature, we would expect the two types of water to be completely mixed if we returned at the end of time. Given the uses to which we will put the answer, however, the question must be

quantitative—HOW FAST does water (or anything else) diffuse? The physical chemist Fick formalized the requisite mathematics, beginning with his first law, which was published mid 19th century. There are three points that we can make—points that must be considered in our discussions of water relations, of gas exchange, of stomatal physiology, of ion transport, &c.—so commit them: (a) the driving force for diffusion is the concentration gradient, which is $\delta C/\delta X$—the difference in concentration divided by the distance. This means that the driving force for a large concentration difference operating over a large distance can be small, whereas the driving force for a small concentration difference operating over a small distance can be large. As an example, consider the electrical potential difference (PD) across biological membranes. The actual PD is small, say, 100 mV—or 1000x smaller than the PD between the "hot" wire in a wall socket and ground. However, there is a large driving force resulting from the PD simply because the membrane is so thin (ca. 3.5 nm), which calculates to about 30 000 000 volts per meter! (b) The time required for diffusion is proportional to the square of the distance. This is a very very important relationship, one where intuition fails us. We can ask whether diffusion can account for the movement of sucrose, which is produced in a leaf and moved to the root. The answer is no; diffusion has been calculated to be 10 000x too slow. We can ask whether sucrose can diffuse through the apoplast, from one leaf cell to another; the answer is yes, easily yes. By way of example, I have calculated that a point source of sugar in a 10-nL aqueous droplet (roughly 100x the volume of an average plant cell) would diffuse to 99% homogeneity within about 2 s. Nobel (Biophysical Plant Physiology and Ecology) has calculated that it would take 0.6 s for small molecules to diffuse 50 µm and reach a concentration there that is 37% of the value of the origin. Others (Taiz/Zeiger: Plant Physiology) have calculated that it would take about 24 years for a point source of a low-mol-wt substance to diffuse the length of a corn leaf. (This last end-point was calculated based on the concentration of the distal point reaching one-half the concentration of the point-source.) The overall conclusion to be reached is that diffusion over cellular distances is easily a mechanism to explain movement, but diffusion is woefully inadequate as a postulated mechanism used for explanation of long-distance transport. (c) The rate of diffusion is highly dependent on the nature of the diffusing substance and the medium through which it diffuses. Thus, for each situation, there is a diffusion coefficient. E.g., the rate of lateral diffusion of an integral membrane protein across the fluid lipid phase will be quite different from the rate of diffusion of a water molecule in air. Easily, this factor can vary as much as four orders of magnitude. As an example, the value of D for CO_2 diffusion in air is $1.5 \times 10^{-5} \cdot m^2 \cdot s^{-1}$ whereas the correlate value for a globular protein (Mr=15 kD) in water is 10^{-10}. Thus, the rate of diffusion of a sugar molecule in water (see above) will be much faster than the rate of diffusion of this same molecule through the structured cytosol. (N.B. This foregoing explanation should be relied on, and dependence on your text on this point might be confusing.)

(3) The process of osmosis can account for the net movement of water. In brief, and correctly, the presence of a solute in an aqueous solution lowers the chemical potential of the water in the solution. Thus, water will move from a region that contains a low concentration of the solute (relatively higher chemical potential of water) to a region that contains a high concentration of the solute (relatively lower chemical potential of water). We will come back to osmosis later when the colligative properties of a solution are covered, and you may wish to consider that osmosis comprises diffusional processes and bulk movement. At present, I will simply make two points. First, it is incorrect to say (as virtually all textbooks do) that liquid water moves from its region of high concentration to its region of low concentration, unless it is explicit that concentration is not defined, as it usually is, as (amount of substance X)/volume. Briefly, depending on the solute, addition of the solute to water may result in dilution of the water, or a contraction in the volume of the water. Second, despite more than a century of thinking about the processes, scientists argue about what the solute does to water.

Overhead 3: Science (magazine) articles.

Given above a description of the types of water movement, now let us turn our attention to some of the factors that affect the movement of water:

(1) Pressure, as we noted above, will drive bulk flow of water. From our experience, we know that pressure will drive bulk flow, *regardless* of the distribution of the solutes in the system.

(2) Temperature will influence the movement of water for several reasons. E.g., gaseous water molecules move faster when they are hot. Another example, apparent, is that water undergoes phase transitions—water molecules themselves move easily in the liquid phase, but not in the solid phase, whereas proton movement is about 50x higher in structured ice than in liquid water.

(3) The term “matrix effects” describes the interaction of water with surfaces. Usually, we can ignore these effects in normal vegetative growing parts of a plant—i.e., before matrix effects come into play, the specimen must be pretty desiccated. We must consider the matrix effects in some soils (e.g., to dry clays, which have a negative charge to which the positive partial charges of H in the polar water molecules are attracted). In seeds, which may have a water content of only 5-15%, starch grains are bound tenaciously to water. In fact, the matrix effect primarily accounts for water uptake by dry seeds in the process of germination (water uptake that initiates germination is called imbibition). Keep in

mind that many surfaces are always in attraction to water, but that water is so much more tightly bound that we are usually dealing in our discussions with the water away from surfaces.

(4) Differences in the concentration of water from one region to the next can be an important factor to consider. More precisely (but not as a matter of routine in this course), we should consider the effective concentration, or activity, for a liquid. For a gas, we will express the concentration as pressure (or, if we wished, more precisely, fugacity—the effective pressure). Since we may be only interested in a particular molecular species (e.g., water vapor) in a gas (e.g., air), we must specify that the pressure under consideration is that of the water, and not the total pressure. Thus, we say that the "partial pressure of water" is such and such. In brief summary, the driving force for gaseous water movement is the concentration gradient, but in solutions of liquid water at the same pressure, the osmotic potential will be an experimentally validated approach, despite, as you saw earlier, some theoretical arguments. (It may be of interest that the empirical data on which the equations are based were gathered by a German botanist [Pfeffer] at the University of Tübingen toward the end of the 19th century.)

(5) As mentioned, solutes have an effect on the chemical potential of the solvent. Consider that addition of a solute (e.g., sucrose) to pure water lowers the chemical potential of the solvent water so that pure water (the reference state) in a different region (e.g., across a membrane) would have a propensity to redistribute to the solution. (For reasons of linguistic simplicity, I will commonly speak teleologically: water wants to move from a weak solution to a strong solution.) At the expense of redundancy, addition of the solute affects the chemical potential of water *independent* of the water concentration *per se* (expressed as mol water/volume). The effect of an **ideal** solute on the solvent is independent of the nature of the solute—it does not matter whether the solute is large or small, whether it is charged or not, &c. The important consideration is to be aware of the number of moles of particles of the solute. E.g., 1 mol of sucrose yields 1 mol of particles. However, 1 mol of NaCl yields (we'll say) 2 mol of particles because NaCl dissociates in solution. We refer to the effects of the solute on the solvent as colligative (meaning, "collected together") properties, which manifest themselves in four ways. Since the colligative properties also allow us to determine the water status of a solution (e.g., expressed plant sap), we will review them:

Overhead 4: Colligative properties of water

(a) The first property is elevation of boiling point of a solution (ΔBp). The overhead shows the "form" of the equation. The equation expresses two important relationships. (a) the elevation of boiling point is directly proportional to the molality of the solution. (Molality, recall, is the number of moles of a substance per 1000 g water. In contrast, recall, that molarity is the number of moles of a substance in a volume of 1 liter of solution.) You can not simply interconvert the two, unless you have data for the particular solute. E.g., a one molal solution of glucose contains 180 g glucose plus 1000 g water. Knowing that glucose in a solution displaces in volume (expressed in mL) about 0.6 its mass in grams, and letting 1 g water=1 mL water, a one molal solution made with one mol of glucose will have a volume of about 1108 mL. Thus, a one molal solution of glucose will be approx. 0.9 molar. The key point, of course, is to know the displacement ($0.6\ \mathrm{mL} \cdot \mathrm{gm}^{-1}$), which permitted the calculation.) The second point is that the elevation of boiling point is inversely proportional to the latent heat of vaporization, which for water is large (nominally, $540\ \mathrm{cal} \cdot \mathrm{gm}^{-1} = 10.5\ \mathrm{kJ} \cdot \mathrm{mol}^{-1}$, which is the highest for any liquid). The consequence is that the boiling point elevation is small. (These facts, put to you formally here, are the same as those transmitted to you in a qualitative sense in earlier courses—e.g., sweating cools.) Finally, note that the temperature at which pure solvent boils exerts only a small effect. Compare the effect: 60° F (= 288° K) vs. 80° F (= 300° K). Your calculations will show that this rather large temperature difference will change the boiling point elevation by only about 7 %.

As mentioned, the boiling point elevation is rather small, so it is difficult to use this colligative property to measure the concentration of a solution. Consider xylem sap, which, let's say, is 10 mmolal. To obtain a precise measurement (± 10 %) would require that we determine with confidence a change of 1 mmolal—which is equivalent to 0.000 5° C.

(b) The second colligative property of an aqueous solution is freezing point depression (ΔFp). Note that the form of the equation is similar to that for boiling point elevation, but that the latent heat of fusion (about $80\ \mathrm{cal} \cdot \mathrm{gm}^{-1}$) is much smaller than the latent heat of vaporization. The consequence is that the molal value is higher, 1.8° C per molal. You will also note that a solution is liquid over a larger range of temperatures than is pure water.

(Any discussion of bare facts must, of course, have some qualifications. Were you to attempt to measure either of the above colligative properties, it would be important to evaluate the particular system under consideration. E.g., it would be pointless to measure the freezing point depression if the solute solubility is changed significantly by temperature. I.e., if one has a 25° C solution, and lowers the temperature and finds that a precipitant forms, she should stop. Similarly, if the solute vaporizes during heating, a boiling point elevation could not be found directly.)

(c) Vapor pressure is a method of expressing the concentration of a gas species that is in exchange with the liquid phase of the same chemical. I.e., liquid in a closed container will evaporate until the gas over the liquid is saturated (a point at which liquid molecules escaping to the gas phase are equal to the gas phase molecules that are returning to the liquid phase.) An aqueous solution has a lower saturating vapor pressure than pure water. Quantitatively, the solution vapor pressure is directly proportional to the mol fraction of the water. The effect is small, however, because water is so concentrated. Return to our example of a one molal solution of glucose. The numerator is 55 (=mol water per 1000 gm); the denominator, it follows, is 56 (55+1). In brief summary, then, one can calculate that there is about a 2 % change in vapor pressure per molal of solute.

Saturating vapor pressure of water varies a great deal with temperature:

Temperature (°C)	Saturating Vapor Pressure (mm Hg)
0	4.6
5	6.5
10	9.2
15	12.8
20	17.5
25	23.7
30	31.8

Alternatively, we say that air that contains a partial pressure of water of 6.5 mm Hg has a dewpoint of 5° C i.e., if air containing 6.5 mm Hg water-vapor pressure is cooled below 5° C, dew will form. We also express the water content of air by RH, which is the amount of water vapor present divided by the saturating vapor pressure. Thus, air that contains 31.8/2 = 15.9 mm Hg at 30° C will have an RH = 50%.

(d) Solutions exhibit the colligative property osmotic potential (sometimes, osmotic pressure). The effect is large, as the form of the equation shows, being about 2.5 $\mathrm{MPa \cdot molal^{-1}}$.

Overhead 5: Osmotic potential

This overhead is yet another portrayal of an osmometer. From earlier courses, you know that if the inelastic differentially permeable bulb containing a solution is lowered into pure water, water will move from the pure water (the region of highest chemical potential of water) into the solution (the region of lowest chemical potential of water). In this simple system, there are only two considerations: (i) the concentration of the solute, and (ii) the height of the water column. Net movement of water will cease when the hydrostatic pressure is equal and opposite of the osmotic potential. By way of example, if the solution is one molal, the osmotic potential of the solution is about -25 atmospheres, and at equilibrium, the water column must exert a balancing pressure of +25 atmospheres—or nominally 250 meters in height. Obviously, osmotic potential is a powerful force. (As I alluded to earlier, you may wish to consider osmosis as demonstrated with the osmometer a composite of two types of movement, viz., diffusion of water across the membrane and bulk movement of water up into the capillary.)

How can and do plant physiologists express the water status of a plant? The simplicity of this question belies the complexity of the answer that follows. As a preview—at the end of this section, the universal method—WATER POTENTIAL (Ψ)—will be described. First, we will review other approaches, some of which still have valid applications.

(1) Relative water content (RWC) is defined as the (water content of the tissue)/(water content of the tissue at full turgidity). Found infrequently in the literature as an actual measurement of the water status *per se*, this method still finds some applications. A significant limitation to this approach is that it is only an "internal" measure. E.g., we may compare the RWC of one tomato leaf to the RWC of another tomato leaf, but a comparison of the RWC of xylem to the RWC of tomato leaf would make no sense. Returning to our example of the osmometer, recall that the water in the bulb is at thermodynamic equilibrium with the bathing water. Yet, a contrived RWC would be different. How could you predict the direction of spontaneous water movement, using RWC of roots and shoots? The answer, of course, is that you could not.

(2) The tissue water content (which ranges from very low in seeds (5-15 %) to very high in succulent tissues (>90 %) suffers from the same disadvantages as RWC. Like RWC, however, there are still some practical, limited uses. E.g., in experiments designed to elicit the synthesis and accumulation of the plant growth regulator ("hormone") in leaves as a response to water insufficiency, we and others in some experiments dehydrate a leaf under a fan until the leaf has lost 10% of its mass. This simple protocol allows us non-destructively and reproducibly to water-stress leaflets to the same extent, day after day.

(3) Suction pressure (aka suction force) is only occasionally used nowadays. It is thermodynamically unsound, connoting, as it does, that water is being pulled. While this notion may be valid in an explanation of the ascent of sap in xylem, it does not generally provide the basis for an explanation of water movement.

(4) Diffusion pressure deficit is a term derived from one of the colligative properties of a solution, viz. Raoult's law, which stated that the vapor pressure over a solution is decreased in direct proportion to the "dilution" of water expressed as the mole fraction.

(5) **WATER POTENTIAL** is the universally accepted and most common method of expression of water status in plant physiology. The problem, simply stated, has been to develop a method or system that lends itself to easy measurement, that permits valid comparisons among diverse tissues, that is

thermodynamically sound. The methods described above fail in one way or another to meet all these criteria.

Rather than develop the concept of water potential in a rigorous mathematical way, I will simply try to explain the logic that led to the concept and provides you with an important mathematical implication. (a) As a first step, consider the chemical potential—as mentioned earlier, the chemical potential is a thermodynamic intrinsic property (like temperature) of a particular chemical species. In our discussions, we have considered only the thermodynamic status of water itself because we want to be able to predict the spontaneous direction of water movement. An intrinsic property is independent of the quantity. Return to the osmometer—it would not matter if the bathing reservoir were doubled in volume (as long as gravitational effects were maintained). By definition, chemical potential is the partial molal Gibbs free energy in a defined system. That is a high-falutin expression that you really do not need to understand for the purposes of this course. (Or, you can drive an automobile without understanding pyrolysis, but you do need to keep an eye on the gas gauge.) Suffice it for present to know that processes tend to move to the lowest free energy. Water will have the propensity to move from a region of high chemical potential of water to a region of low chemical potential of water, because that movement is down a free energy gradient. (b) There are many factors that can influence the chemical potential. Return to the osmometer and you see two factors right away—the presence of the solute in the bulb lowers the water chemical potential (and makes water "want" to move in). This idea is important: the presence of a solute always lowers the chemical potential of water. A second factor observed in the osmometer is that positive hydrostatic pressure increases the chemical potential of the water. I.e., from the initial state to the final state, the chemical potential in the bathing solution was unchanged—no solutes were added, the pressure was unchanged, &c. Thus, at equilibrium, the chemical potential of the water in the bulb is equal to the chemical potential of water of the bathing solution. At this point, there is no net movement of water molecules. Now—and this is important—imagine that you reached into the bathing solution and pricked the bulb, making a large hole. What would happen? Obviously, the water would flow through the hole pricked in the bulb. Thus, from your own experience, you know that the concept of chemical potential can not be usefully applied to predict bulk water flow. (This is not an inconsistency, just a misapplication of the concept of chemical potential, which can only be used to predict diffusional or osmotic water movement). (c) A "problem" with chemical potential is the difficulty of measuring it. Plant physiologists have become accustomed to thinking of the water status of plants in pressure units, just as we did with the osmometer. At the expense of redundancy, we can measure the pressure resulting from gravity in the capillary and use that to infer the osmotic potential ("pressure") of the solution, since these parameters must be equal, but opposite in sign, if the solution water is at equilibrium with pure water. The solution to this "problem" was the development of a new concept—a quantity that would be thermodynamically sound (i.e., based on chemical potential) and simple to measure. The concept, denoted by the Greek letter Ψ (say psi), is called the water potential.

$$\Psi = (\mu_A - \mu_O)/V_w$$

Alternatively, in words, water potential = [(chemical potential of the water under consideration) - (chemical potential of water at the reference state)]/(partial molal volume of water).

Overhead 6: water potential

There are important implications of this definition: the reference state of water is pure water at normal atmospheric pressure and at the same temperature as the water under consideration. The unit is pressure. (a) You have already noted that chemical potential can not be used to predict bulk flow. Since water potential is based on chemical potential, water potential can not be used to predict the direction of bulk flow. (b) The temperature **must** be a constant; this requirement arose from the need to simplify the mathematics to manageable proportions during the derivations. In other words, you can not use water potential to compare the water status of one leaf at 25° C to another leaf at 20° C. (c) There is no absolute water potential—the measurement is always made against a reference state. In other words, pure water at 25° C and under 2 atmospheres of pressure will have a water potential of 0.2 MPa. Similarly, pure water at 35° C and under 2 atmospheres of pressure will have a water potential of 0.2 MPa. However, you can not compare these two values directly because they are measured against a different reference state. (d) Water potential can be applied to solutions, but not to gases. The reason is simple: the derivation of water potential included a term for partial molal volume. Gases do not have a defined volume. Nevertheless, most textbooks and most plant physiologists apparently do not recognize this point, perhaps because they have not followed the derivations. You will encounter this common misconception and provide a quantitative assessment.

It is customary (see overhead) to consider that water potential consists of three terms that are additive:

$$\Psi = \Psi_P + \Psi_S + \Psi_M$$

Or, in words, water potential = pressure potential + osmotic potential + matrix potential

Matrix potential, as we discussed earlier, can be ignored for many tissues. Different algebraic conventions and different abbreviations are used in various places. We will follow the convention adopted by the premier journal, *Plant Physiology*, as it is shown on the overhead.

The following points should be taken: (a) Ψ_P may be positive or negative or zero. (b) Ψ_S will always either be zero or negative, if there is a solute present. At the expense of redundancy: (a) Do not use Ψ to attempt to explain the bulk movement of water. Think about this idea for a moment: Water in the xylem and water in the phloem exist side-by side. As an example, in the leaf, the xylem water potential is approximately the same as the phloem water potential (otherwise, water would move osmotically across the sieve-tube membrane from one region to the other). Similarly, the xylem water potential in the root is approximately the same as the phloem water potential there (otherwise . . . .). We know that the overall movement of water is from the root to the air. We know, also, that there is solution flow in the phloem to the roots to feed this sink region. Obviously, one cannot simultaneously explain upward and downward water movement by the concept of water potential. (b) Do not use water potential to attempt to explain gaseous water movement, because water potential has a volume term in it and gases do not have a specified volume. (c) Water potential is measured against a reference state (i.e., there is no absolute value for water potential—the value expressed is the difference between the water or solution under consideration and the reference, which is PURE WATER AT ONE ATMOSPHERE OF PRESSURE, AND AT THE SAME TEMPERATURE AS THE WATER OR SOLUTION UNDER CONSIDERATION.

Overhead 7: Various effects on water potential

This overhead summarizes many of the ideas that you need to understand on the theory and some of the practice of water potential.

Consider the top panel. Pure water at one atmosphere of pressure has a water potential of 0 Pa, because it does not differ from the reference state. N.B. The temperature must be constant! A solution at atmospheric pressure must have a negative water potential. Pure water that has a pressure exceeding one atmosphere must have a positive water potential. A solution under pressure may have a negative or a positive water potential, depending on the magnitude of the pressure (how far it differs from the reference state of one atmosphere) and the solute content, this last which can be calculated from the van't Hoff equation.

Consider the middle panel. Again, pure water at atmospheric pressure has a water potential of 0. If we submerge the inelastic bulb having the differentially permeable membrane—recall our osmometer—into the water bath, water will diffuse in. As mentioned earlier, application of pressure to the capillary tip of the system at equilibrium will cause water to diffuse out. Now, let us express quantitatively the same idea in terms of water potential. Say our solution inside the osmometer is 1 molal, the osmotic potential will be -2.5 MPa. I.e., the osmotic potential differs from the reference state by -2.5 MPa. On the other hand, the pressure potential is at one atmosphere and therefore does not differ from the reference state. Thus, the water potential of the solution is -2.5 MPa + 0 MPa = -2.5 MPa. The water potential of the bathing solution is 0 MPa. The driving force for water movement into the bulb is the water potential gradient, or -2.5 MPa/(thickness of the inelastic differentially permeable membrane). When the system comes to equilibrium—i.e., there is no driving force for water movement, and thus no net movement of water—the water potential of the solution and the bathing water must be equal. Since the bathing water remains at the reference state (pure water at one atmosphere of pressure and at the temperature of the water (or solution) under consideration), we know that the osmometer solution must also have a water potential of 0 MPa. Since we stipulated that there were no volume changes in the solution, the solute potential of the solution remains at -2.5 MPa. Thus, the pressure potential must at equilibrium be +2.5 MPa.

Consider the bottom panel. The water potential of well-watered soil is near zero. (The solute content is relatively low and matrix influences do not count if there is a bulk-water phase. Hydrostatic pressure in this example is negligible; however, there can be considerable hydrostatic pressure in some instances, as exemplified by water flow from a spring.) The solute potential for a leaf is negative, but the value (ca. -1.8 MPa) shown on this overhead (i.e., too much solute)—a more typical value would be perhaps -1.0 MPa (general range =-0.5 to -2.5 MPa). It is important to note, however, that solute potential can vary a great deal, and some very low values (-9.0 MPa, which corresponds to approximately 3.7 molal) have been reported. Plant cells, as you know, are under positive internal pressure. Perhaps a typical value would be about 5 atmospheres, or +0.5 MPa. By way of example, the broad bean plants that we grow in pots in growth cabinets have an overall leaf water potential of ca. -1.5 MPa. (We'll return to these “typical values” later, as a means of emphasis.)

Obviously, the “reference” values given above can only provide notions concerning the water status and components of water potential in particular cells of the leaf. As we mentioned earlier, the tracheary elements and the sieve-tube elements are very near each other, both being in vascular bundles. Tracheary elements, recall, are dead, and contain the so-called xylem sap, which has only a low concentration of solute. Sieve-tube elements have a high internal pressure. These cells (tracheary elements and sieve-tube elements) clearly must have approximately the same water potential—the sieve-tube membrane separates them—otherwise water would flow osmotically from the region of high water potential to the region of low water potential. The conclusion, of course, is that the components of water potential are very different in the two regions. Let's say that the leaf water potential is -0.6 MPa, which implies that all cells of the leaf are near that value. In this case, the pressure potential of the tracheary elements is actually near -0.6 MPa (or ca. 6 atmospheres of negative pressure, or tension). In sharp contrast, the sieve tube elements have a high solute content, in this example from experiments on morning glory vines, the sucrose alone accounted for a solute potential of -0.4 to -0.8 MPa. Adding in the solute potential contributed by other components of the phloem sap (e.g., potassium salts), one easily infers that the pressure inside a sieve-tube element must be minimally several atmospheres. (As an incidental point, calculations suggest that there must be a pressure gradient of about 2 atmospheres per meter to drive mass flow in the phloem.)

In conclusion, let us examine some "memorable"values for water potential in the soil-plant continuum for a transpiring plant:

Location	Ψ (MPa)
moist soil	-0.1
root	-0.2 to -0.4
shoot	-0.5 to -1.5
leaf	-0.5 to -2.5
air	very very dry

There are two take-home messages: (a) the oft-stated fact that the water potential gradient is the driving force for diffusional (osmotic) water movement. Thus, in any particular situation that describes a transpiring plant, the water potential must progress more negative along the path; i.e., the soil water potential must be higher than that of the root, which must be higher than that of the stem, which must be higher than that of the leaf. (b) The difference in the chemical potential of water in the leaf and the air is humongous. Although I have pointed out that use of water potential for expression of the water status of gaseous water is problematical, **if** we accept (for perspective) the relationship given most texts, we would calculate that the water potential of air would be in the range of -100 MPa. Notwithstanding the reservations, you should put firmly in your mind that the propensity of water to move from the leaf to (even moist) air is the large driving force in the path. It is this large driving force that "succeeds" in overcoming the resistance to water in the transpirational pathway.

The preceding green talk allowed a transition between the theoretical aspects of water potential and the more pragmatic applications of the theory to plants. Now, we will examine the pathway of water movement in plants.

Overhead 8: Root tip & Transpiration as a function of root surface

This overhead, to jog your memory, shows the organization of a root tip. Study the 3-D aspects of the root, and recall that there is an "inner skin" that forms a tube around the vascular tissue, wherein lies the xylem, which is in apoplastic continuity with the remainder of the plant. Also, note the abundant root hairs, which as you know, are epidermal-cell protuberances that erupt on the mature side of the elongation zone. The root hairs increase the surface area of the root, and thereby facilitate transport of soil solution inward. (Rupture of these root hairs during transplanting may decrease the surface area of the root by 60%, which is why seedlings must be given special attention for a few days following transplanting.) The "ancient" data on the bottom right of the overhead shows that the rate of transpiration can be limited by the root-surface area. As the ratio (root surface)/(leaf area) increases, so does the transpiration rate of the leaf (expressed on a leaf-area basis).

Overhead 9: Root cross-section

The root cross-section shows the classical view that soil solution or water moves into the root apoplastically (i.e., taking a cell-wall path, around the membrane-bound space) until it reaches the endodermis. (In moist soil, the soil solution itself may be in direct contact with the apoplast; in drier soil, water may "distill" over short distances to the root hair.) A band in the cell wall around each endodermal cell, called the casparian strip, is impermeable to water flow, and, therefore, constitutes an aqueous discontinuity in the apoplast. At least at this point, there must be transmembrane movement of water. What about the solutes in the apoplast? Given an aqueous discontinuity in the apoplast, they, too, must cross a membrane if they are to move further. However, biological membranes are not indiscriminate with respect to the solutes they pass. Thus, and importantly, the endodermis represents a barrier and provides selectivity to the contents of the tracheary elements. Were the endodermis to be absent, deleterious as well as required nutrients would be swept to the leaves via the xylem.

Evidence over the past few years indicates that in most plants, the endodermis is not the first barrier to solution flow in the apoplast. Most plants appear to have an exodermis, located just beneath (i.e., inside of) the epidermis. This exodermis functions like the endodermis. It may turn out, as further research is conducted, that there are two sites of discontinuity in the root apoplast.

Transmembrane movement of water is mostly through so-called water-channels, or aquaporins. Although the idea of water channels dates back to the 1950's, it was only in the mid-90's that we recognized their importance in plants. They were discovered by homology, and then only expressed in nematode-infected roots. We now know that aquaporins represent a large gene family, and can be one of the most abundant proteins of a plant membrane, such as the vacuole (where it was know as the Tonoplast Intrinsic Protein (TIP) before its function was revealed to us.) They are widely distributed and apparently can be modulated by phosphorylation. Mechanistically, some function by electro-osmosis. These channels take advantage of a large driving force for a particular ion to move across the membrane. Then, they open and in the process of facilitating ion transport, water is drug along. Others, perhaps most (as inferred from animal studies), do not rely on electro-osmosis. The high conductance of these channels implies a genuine flow of water (i.e., bulk flow), but osmosis as well as bulk flow can drive this water movement. Obviously, thermodynamic concepts concerning these channels are murky.

Think for a moment. For the sake of simplicity, consider a root without an exodermis. (Your thoughts would reach the same conclusion, but by a longer path if you were to consider plants with an exodermis.) A root **can** perform like the osmometer that we spent so much time with. Solutes, particularly ions, are actively taken up by the roots (i.e., these solutes are removed from the apoplast by the endodermal cells and excreted on the inner face of the endodermis—this is the mechanism by which, e.g., potassium is taken from the soil and transported to the leaf). The higher solute content of the apoplast on the inside would result in a lower solute potential; water would move in osmotically. *Viola* . . . root pressure is generated, analogous to the situation with the osmometer. Recall the effect of a solute on the water potential (the van't Hoff equation); by way of example, a dilute solution of 10 mmolal would have a solute potential of -0.025 MPa, enough to maintain a water column of nominally 8 feet. (Again, the huge impact of the solute on water is realized!) We will return to root pressure in a few moments.

Given an aqueous solution in the dead tracheary elements, how can we account mechanistically for the ascent of sap in plants? Let us consider some of the possibilities: (a) capillarity—upward water movement that is driven by the adhesion of water molecules to the surfaces of the cell-wall polymers. Whereas capillarity is real, it is insufficient to account for upward water movement more than about 0.5 meters, and certainly is not a universal mechanism. (b) root pressure—above, we provided a mechanism for root pressure, and indeed it is a naturally occurring phenomenon. The highest pressures observed are about 0.5 MPa, which is not enough to account for sap ascent in the tallest plants. More frequently, root pressures are absent or relatively small (say, 0.01 MPa), besides, we know that shoots with excised shoots will transpire and therefore root pressure is not required for sap ascent. (As a matter of interest, you sometimes observed root pressure in your daily lives. Ever notice small droplets of water along the margin of some leaves (e.g., grasses, strawberry) in the morning? Overnight, transpiration is low (because the stomata are closed and because there is typically a smaller driving force for evaporation during the night) and root pressure pushes water past the tracheary termini in the leaf. Water is transported out of the leaf by special structures called hydathodes. A second example, one that you will want to avoid, is "bleeding" following pruning. Some plants, particularly vines like muscadines, and walnuts, are particularly "bad" in this regard.) (c) barometric pressure—potentially a mechanism, as it functions in a surface pump. (The pump reduces pressure in the pipe and atmospheric pressure pushes the water into and up the pipe.) As we calculated earlier, atmospheric pressure can support a column of water only about 10 meters tall, and this mechanism, therefore, can not be a universal explanation of sap ascent. (d) pumping stations—various organisms have devised disparate pumping mechanisms such as the heart and the diaphragm, but plants have not. In any case, tracheary elements are dead. (e) Cohesion Theory—this theory states that evaporation of water from leaf cell walls creates negative pressure (or tension) in the xylem and that a pressure gradient (albeit composed of negative pressures) lifts the water to the top of the plant.

Overhead 10: Cohesion Theory of Sap Ascent

Critical evaluation of this theory requires that at least two elements be demonstrable. First, it must be shown that xylem sap is under tension. This demonstration is straightforward. A shoot is excised (or shot into with a high-powered rifle, as Scholander did!). If the xylem is under tension, the water column in the tracheary elements will have retracted (not because water can be stretched, but because the tracheary-element walls are modestly collapsed). Thus, the cut shoot is placed in a pressure bomb with the excised stump protruding. Pressure is applied, which squeezes the shoot until the tracheary-water column is driven to the cut surface. The pressure required is the balancing pressure of the xylem. Values as negative as -80 atmospheres have been reported. Second, there must be physical evidence that water has the requisite cohesive strength. Two typical experiments are cited. Water has been placed in an S-shaped capillary and centrifuged. The centrifugal force "pulls" the water column away from the rotating axle. In this manner, under the relevant conditions, as much as 264 atmospheres of pressure were required to break the column. This value is in clear excess of theoretical requirements and the empirical values cited above. Another way to demonstrate the large cohesive strength of water is to separate two steel plates that are held together by a thin film of water. This experiment was in corroboration of the centrifugation experiment. (You, too, have done a version of this experiment as you attempt to separate two "stuck" microscope slides in lab!)

Tracheary elements comprise two types of cells, as was discussed in the anatomy review. Vessels—short, fat cells that are stacks of vessel elements, which have perforated end walls—are most efficient at transport, because they have less resistance to water flow. (Indeed, they offer one to two orders of magnitude less resistance than do tracheids.) Inextricably coupled to the reduced resistance that results from the larger diameter of the vessel (compared with tracheids) is the increased susceptibility to cavitation, or bubble formation from an erstwhile dissolved gas. Once a bubble forms, transport through that cell stops until (or unless) continuity of the water column is restored. (Because of the surface tension of water (a property consonant with its high cohesion), the gas bubble is contained within a single cell—being unable to spread from cell to cell, which would spell death to the plant.) As implied, in some cases, apparently, the bubble is redissolved, e.g., by root pressure at night. Tracheids, found in all vascular plants, might be thought of as more specialized for support than are the vessels, but they also are less susceptible to cavitation. It may not be coincidence that the tallest plants are gymnosperms like redwood, which fits the generality that this first taxon lacks vessels.

Our understanding of water flow within the leaf—from the vascular tissue to the atmosphere—is murky. There are several possible routes, at least for some plants. What is (or are) the evaporation site in leaves? A controversial postulate (of which I am a fan) is that water evaporates from the inner walls of guard cells. This phenomenon is called "peristomatal evaporation." Some think that water evaporates directly from the vascular tissue itself; this low-resistance pathway could not occur in the plants that have suberized bundle sheaths. Others think that the mesophyll cell walls—having a large surface area—are the primary sites of evaporation. The large surface would, of course, considered alone, promote water transport to the gas phase; however, it has been experimentally shown that the intercellular leaf spaces are very moist, almost 100% RH, so the driving force for evaporation from the mesophyll cell walls is small. It is believed that the apoplastic route for water movement in the leaf is the favored one because of its presumed lower resistance to water flow. The experimental rationale (squeezing water out of a leaf in a pressure bomb is difficult but extrusion of water from the excised petiole is easy if the edge of the leaf is cut away and the leaf is submerged in water) to support the belief fails to control for the possible difficulty of compressing the leaf.

Given the important uses to which the answers are put, it is natural that a great deal of effort has been devoted toward the development and refinement for methods of measuring water potential. Given our limited time, we can only take a cursory examination of the methods: (a) psychometry—the tissue is placed in a closed chamber and allowed to remain there until the tissue water and the gaseous phase reach equilibrium (remember Raoult's law?). Since the tissue water has a lower chemical potential than pure water, the air above the tissue will be at less than saturating vapor pressure for that temperature. The dewpoint of the air is measured, typically by use of a thermocouple junction. There are several variations of the exact methodology, but all these approaches suffer from the large variation of vapor pressure with temperature. This fact means that temperature must be stringently controlled to attain adequate precision; thus, this method is usually relegated to laboratory settings, and, generally, is not used in the field. A particular advantage to this method is the ease with which the overall water potential can be measured as well as the components. The first measurement, as mentioned, is of intact tissue, and gives the overall water potential. The second measurement is taken after the tissue has been disrupted, e.g., by freezing. Breakage of the cell walls relieves pressure, and thus, the pressure component is the reference (i.e., one atmosphere). The second measurement, therefore, is a measure of the **average** solute potential of the leaf. The difference between the first and the second measurement is the pressure potential. (b) pressure bomb—we have already noted how the water potential of the leaf can be measured with a pressure bomb.

With certain tissues (those that can withstand without collapse the requisite pressures), other parameters can be measured with the pressure bomb by following the kinetics of water efflux with pressure steps. These esoteric applications are reserved for the experts! (c) pressure probe—first used with giant algal cells, and later adapted to "real" plant cells by Zimmerman, Stuedle, Tomos, and others who have a flair for the difficult, pressure probes are small pipettes that are inserted into cells. The pipettes are fitted with a pressure transducer, thus yielding pressure potentials. These methods, combined with miniaturized versions of approaches to measure solutes (e.g., nanoliter osmometers) will ultimately provide a detailed evaluation of the water relations at high morphological resolution.

How does water insufficiency affect a plant? At the phenomenological level, this question was sufficiently answered more than twenty years ago. The most sensitive processes, alterations of which can be elicited by a water potential shift of less than 0.5 MPa, are growth, wall synthesis, and protein synthesis. One aspect of growth is cell expansion, which is driven by turgor. At a shift of less than 1.0 MPa, the stress plant growth regulator ABA accumulates. This regulator has effects on many processes, such as stomatal closure, leaf abscission, sugar transfer between cells, seed germination, elicitation of particular proteins and suppression of the accumulation of others. Under high water stress (a shift of 1.0 to 2.0 MPa), some plants produce in abundance low-mol-wt substances that lower the solute potential. (The lower solute potential would cause an overall drop in water potential, so that water would still move into the cells and restore turgor.)

Inroads into an understanding of the mechanistic basis of water stress are slowly being unraveled. Ion channels that are "stretch-activated" have been discovered in plants, and many new proteins that are associated with turgor loss, or ABA, or salt-stress (or some combination of these) are being aggressively studied. Stay tuned.

Appendix: Proportionality relationships between *y* and *x* where $y^b \alpha x^a$.

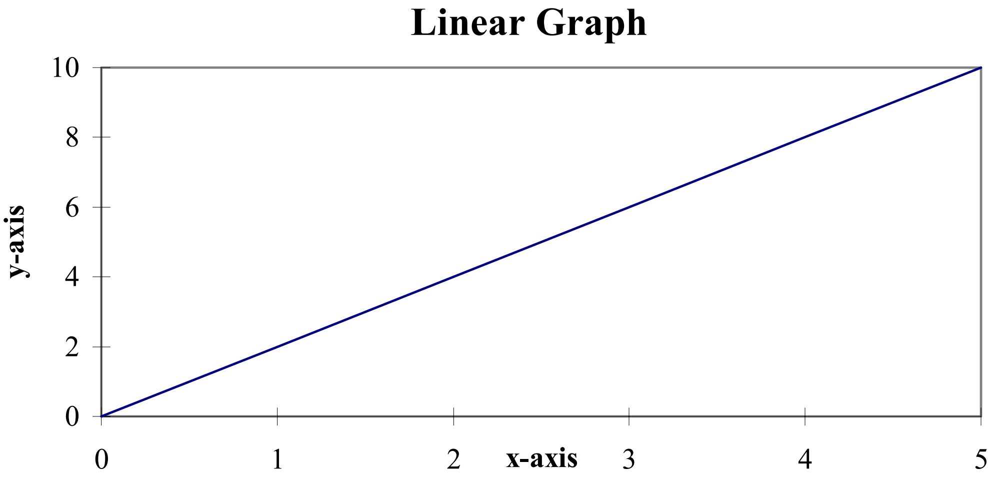
(My thanks to William M. Outlaw for developing this appendix.)

Examples:

1. $y \alpha x$. Here a=1. The resulting plot is linear through the origin.

Question: if $y_1 = 2$ *and* $x_1 = 1$*, what is* y_2 *when* $x_2 = 2$*?*

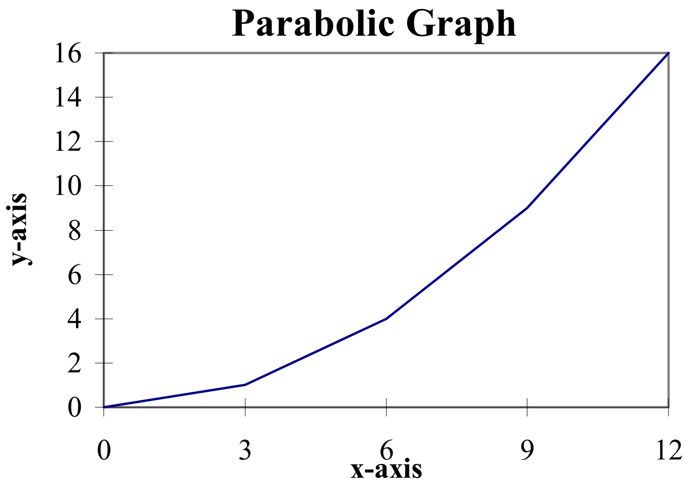
Answer: Use proportionality relationships $(y_1/x_1)=(y_2/x_2)$
With the numbers given: $2/1=y_2/2$*, so* y_2*-2x2=4*
The relationship in this ***specific*** *case is y=2x*



2. $y \alpha x^2$. Here a=2. The resulting plot passes through the origin and is parabolic.

Question: If y_1-1 and x_1=3, what is y_2 when α_2=6?

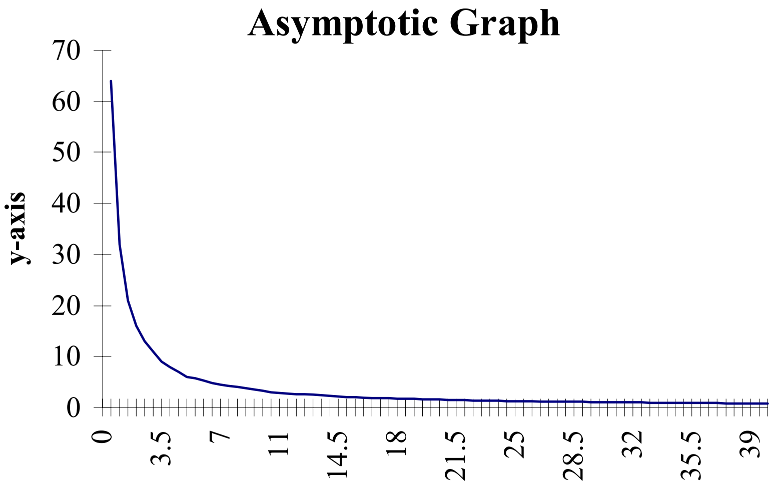
Answer: Again use proportionality relationships: $(y_1/x^2{}_1)=(y_2/x^2{}_2)$
With the numbers given: $1/9=y_2/36$, so $9y_2=1x36$ and $y_2=4$
*The relationship in this **specific** case is $y=x^2/9$*



3. *y* α 1/x. Here a=-1. The resulting plot is asymptotic to both the x and y axes.

Question: If $x_1=4$ *and* $y_1=8$*, what is* y_2 *when* $x_2=16$*?*

Answer: Still using proportionality relationships: $(y_1/(1/x_1)]=[y_2/(1/x_2)]$
With the numbers given: $[9/(1/4]=[y_2/(1/16)]$*, so* $16y_2=32$ *and* $y_2=2$
The relationship in this ***specific*** *case is* $y=32/x$



Appendix: Exponentials and Logarithms

(My thanks to William M. Outlaw for developing this appendix.)

Exponential equations: Definition

Form: $\mathbf{y = ax^n}$
Qualifications: **y** is dependent upon **x**; **a** and **n** are real numbers
Example: $y_1 = 1\text{x}10^{-6}$ and $y_2 = 1\text{x}10^{-9}$ where **a** is 1, **x** is 10, and **n** is -6 and -9, respectively.

Exponential equations: Operations

Multiplication of exponents is characterized by the *addition* of **n** *if and only if* **x** for both is equal

Example: $y_1 \text{ x } y_2 = 10^{-6} \text{ x } 10^{-9} = 10^{-9+-6} = 10^{-15}$

Caution: $10^{-6} \text{ x } 5^{-9}$, for example, does **not** equal 50^{-15}; here the base numbers **x** are not identical and thus addition of exponentials is not allowed

Division of exponents is characterized by the *subtraction* of **n** *if and only if* **x** for both is equal

Example: $y_1 / y_2 = 10^{-6} / 10^{-9} = 10^{-6-(-9)} = 10^3$

Caution: $10^{-6} / 5^{-9}$, for example, does **not** equal 2^3; here the base numbers **x** are not identical and thus subtraction of exponentials is not allowed

Addition of exponents is characterized by a conversion of one exponential into a multiple of the other and the subsequent addition of common multiples.

Example: $y_2 + y_1$. y_2 may be expressed as $0.001\text{x } 10^{-6}$, a multiple of $1 \text{ x } 10^{-6}$ (y_1). So, the addition then becomes $(0.001 + 1) \text{ x } 10^{-6} = 1.001 \text{ x } 10^{-6}$. Likewise, y_1 may be expressed as $1000 \text{ x } 10^{-9}$, a multiple of $1 \text{ x } 10^{-9}$ (y_2). Here the addition becomes $(1 + 1000) \text{ x } 10^{-9} = 1001 \text{ x } 10^{-9}$. These two methods provide identical answers; only the base number **n** of the exponential answer is different

Subtraction of exponents is characterized by a conversion of one exponential into a multiple of the other and the subsequent subtraction of common multiples.

Example: $y_1 - y_2$. y_1 may be expressed, as shown above, as $1 \text{ x } 10^{-6}$, while y_2 is expressed as $0.001 \text{ x } 10^{-6}$. Then, our expression becomes $(1- 0.001) \text{ x } 10^{-6} = 0.999 \text{ x } 10^{-6}$. Similarly, y_1 can be expressed as $1000 \text{ x } 10^{-9}$ while y_2 is $1 \text{ x } 10^{-9}$. Here our answer is $(1000 - 1) \text{ x } 10^{-9} = 999 \text{ x } 10^{-9}$. Again, these two methods give identical answers, differing only in the chosen common base number **n**

Logarithmic Equations: Definition

Form: $\log_{\mathbf{b}}\mathbf{N} = \mathbf{L}$ where $\mathbf{b}^{\mathbf{L}} = \mathbf{N}$

Qualifications: **b** is considered the *base* of the log. For our purposes, we will stick with conventional base numbers of 10 or *e*. **L**, which is dependent upon **N**, is any real number. **N** is defined to be any number greater than zero. *Logarithms of negative numbers are undefined!* In the following discussion, *log* will be restricted to base 10, while *ln* will be restricted to base *e*.

Example: $\log(100) = 2$ because $10^2 = 100$; $\log(0.001) = -3$ because $10^{-3} = 0.001$

Logarithmic Equations: Operations

Addition of logarithms is characterized by the log of the *product* of the **N**'s in each individual logarithmic expression

Example: $\log(100) + \log(0.001) = \log(100 \times 0.001) = \log(0.1) = -1$;
$\ln(100) + \ln(0.001) = \ln(0.1) = -2.303$ because $e^{-2.303} = 0.1$

Subtraction of logarithms is characterized by the log of the *quotient* of **N**'s in each individual logarithmic expression

Example: $\log(100) - \log(0.001) = \log(100/0.001) = \log(10^5) = 5$;
$\ln(100) - \ln(0.001) = \ln(10^5) = 11.51$ because $e^{11.51} = 10^5$

Logarithmic Equations: Hints and Manipulations

1. $\mathbf{a}\log_{\mathbf{b}}\mathbf{N} = \log_{\mathbf{b}}(\mathbf{N}^{\mathbf{a}})$

Example: $5\log(10) = \log(10^5) = 5$; $5\ln(1) = \ln(1^5) = 0$

2. $\log(2) \sim 0.3$. This hint allows us to estimate a wide variety of logarithms without using a calculator

Example: Evaluate log(4) and log(32) without the aid of a calculator
$\log(4) = \log(2 \times 2) = \log(2) + \log(2) = 0.3 + 0.3 = 0.6$
$\log(32) = \log(2^5) = 5\log(2) = 5 \times 0.3 = 1.5$

Logarithmic Equations: Graphical Expressions

Key Points:

1. Logarithmic equations (both log and ln) have x-intercepts at (1,0).
2. Logarithmic equations are undefined for all x less than or equal to 0.
3. Logarithmic equations are **not** asymptotic; with increasing **x** values, **y** values reach to infinity
4. The slope (derivative) of ln(x) at any coordinate is greater than the slope of log(x)