7 Water and Plants

Water is amazing and essential to life on earth. In this chapter, we will explore the many ways in which water is vital to plant life and how we use water as a management tool to improve productivity in many horticultural endeavors. A particularly nice reference on exploring water from many different angles is *Water Structure and Science* (Chaplin, 2011).

Basic Properties of Water in Plants

Water is a phenomenal substance. Without it, life as we know it would not exist. Some of the properties which make it so extraordinary include its specific heat, heat capacity, heat of fusion, heat of vaporization, and density (Table 7.1).

Specific heat

The specific heat is the amount of energy required to raise the temperature of 1 g of a substance by 1°C. It is an intensive variable meaning that it is a property that is independent of the quantity of the substance in question. The specific heat of water, higher than any other common substance, is 1 cal/g/°C. The specific heat of copper is 0.092 calorie/g/°C. So what? This means that it takes almost 11 times (1.0/0.092 = 10.87) as much energy to heat 1 g water from 20 to 21°C compared with heating a penny from 20 to 21°C. If water requires so much more energy for the same mass as copper, where does the energy go? It is stored as potential energy in the water. All substances have a certain amount of internal energy associated with them. This energy is a combination of kinetic (molecular movement) and potential (stored with a capacity to do work) energy. Temperature is a measure of kinetic energy, thus the difference in specific heat of two substances reflects the difference in their potential energy. The large amount of potential energy of stored in water makes anything containing water (i.e. plants) very resistant to sudden changes in the temperature of the surrounding environment.

Heat capacity

Heat capacity is different from specific heat capacity. Heat capacity is the amount of energy required to raise the temperature of a substance (or an object) by 1°C. It is an extensive variable since it relies on the quantity of the substance in question to determine its value. For example, the heat capacity of 1 kg of water is much greater than that of 1 g of water, even though the specific heat capacity is the same regardless of mass.

This is important in looking at plants and their resistance to temperature change, particularly when considering frost injury to sensitive species. Larger plants or tissues have a greater heat capacity then smaller plants or tissues, thus are more resistant to frost injury (this is discussed further in Chapter 9, this volume).

Heat of fusion

The heat of fusion of water is 80 cal/g and is the amount of energy liberated when water freezes. We can use this heat given off when water freezes to measure the lethal low temperature for a number of horticultural crops in low temperature stress studies, for example peaches (*Prunus persica*), cherries (*Prunus* spp.), and azaleas (*Rhododendron* spp.). We also use this heat when using overhead irrigation to protect crops from frost injury. (Note that it is the resistance to temperature change until a total phase transition that a mixture of ice and water has that really protects from a frost.)

Heat of vaporization

The heat of vaporization for water is 540 cal/g and is the amount of energy absorbed when water goes from a liquid to a gas. A tremendous amount of energy is removed from plant leaves as water evaporates from them during transpiration.

Table 7.1. Properties of water that make it important in horticulture.

Property	Value	Importance
Specific heat	1 cal/g/°C	Makes plants very resistant to sudden changes in the temperature of the surrounding environment
Heat capacity	Varies	Makes larger plants or tissues more resistant to frost injury
Heat of fusion	80 cal/g	Allows measurement of freezing point; frost protection using overhead irrigation
Heat of vaporization	540 cal/g	Provides cooling energy during transpiration
Density at 0°C		
Liquid	0.9998 g/cm^3	Allows ice to float and prevents bodies of water from freezing from the bottom up
Solid	0.931 g/cm^3	
Universal solvent		Provides medium for life as we know it
Hydroxyl bond		Absorbs infrared energy making water vapor a potent greenhouse gas

Density

Water is a very odd substance when it comes to density. The density of most solids is greater than their liquid counterparts. The density of water at 0°C is 0.9998 g/cm^3 while ice at the same temperature has a density of 0.931 g/cm^3, thus ice is less dense than liquid water and it floats. Another interesting fact about water is that it has a maximum density of 1 g/cm^3 at 3.98°C. Why is this important? As a body of water cools in response to cool air above it and approaches its freezing point, it becomes denser and when it reaches 3.98°C, it sinks and is replaced with warmer, less dense water from below. Once the entire body of water is at 3.98°C, it will continue to cool and the top layer will freeze when it reaches 0°C (we're not considering freezing point depression cause by any dissolved solutes in the water). Since the ice is less dense than liquid water, it floats. Thus the body of water freezes from the top down. If ice didn't float, lakes, rivers and bays would freeze from the bottom up and probably freeze solid. As it is, the floating ice offers a layer of insulation to the water below, thus bodies of water don't normally freeze solid, but rather only a few centimeters to a few meters deep.

Water in the Environment

Water in the atmosphere

Our atmosphere always has water in it. Rain and fog are important water sources for plants and melting snow is important for recharging groundwater stores or reservoirs for use during the growing season. The energy released or absorbed (fusion and vaporization) during phase transitions of water in our atmosphere are critically important in managing the energy balance of our atmosphere.

Much of the time atmospheric water is in the form of water vapor we don't see. We see products of condensation (clouds, fog, or rain) (Fig. 7.1) or freezing (snow or ice crystals) in our daily weather, but water vapor is essentially invisible. Water vapor is also the most potent greenhouse gas, even though we often hear more about CO_2 and methane (CH_4). Water vapor is such a powerful greenhouse gas because of its hydroxyl bond which absorbs a tremendous amount of infrared energy.

Water vapor content of the air is expressed in a number of different ways: (i) dew point; (ii) vapor

Fig. 7.1. Early morning ground fog in September (New Jersey, USA). Fog forms as the air temperature reaches the dew point just before sunrise after a long night of radiative cooling. Note the fog is close to the ground indicating that this air has cooled to the dew point while air at 4 or 5 m and higher has not and remains above the dew point.

pressure; (iii) specific humidity; (iv) absolute humidity; and (v) relative humidity (RH). The dew point is the temperature at which water vapor in cooling air at a constant barometric pressure will condense to liquid water called dew. At the dew point, the air is saturated with water vapor, meaning that at the given temperature, pressure, and volume, the air could hold no more water molecules.

Understanding water vapor in the atmosphere relies on understanding the concept of vapor pressure. Imagine that you have an open container of pure liquid water that you keep at a constant temperature. At any given time water molecules might be leaving the surface of the water and entering the surrounding air. Additionally water molecules will be returning to the liquid. This movement is based on diffusion and over time if the container is not closed, more molecules would leave than return and eventually your container would become empty due to evaporation. More molecules leave the liquid water than return under most conditions because there are more water molecules in the liquid water per unit volume (in general) than there are in the air above the container and the molecules will move from an area with more molecules per unit volume to an area with fewer molecules per unit volume.

Now imagine placing a lid on your container. This will restrict the movement of water molecules to the volume inside the closed container above the liquid water surface. When the number of molecules leaving the liquid is in equilibrium with the molecules returning to the liquid state, the pressure exerted is called the vapor pressure. Neither the volume of your container nor the surface area of your liquid will affect the vapor pressure. Increasing or decreasing the temperature will raise or lower the vapor pressure, respectively. Saturation vapor pressure is the vapor pressure of the water when the container's vapor volume is saturated with water molecules.

We need to know about vapor pressure because water will move from a plant, primarily from the leaf, into the atmosphere based upon vapor pressure gradients.

We measure and often report the water content of the atmosphere as humidity. There are three different measures of humidity: (i) absolute; (ii) specific; and (iii) RH. Absolute humidity is the mass of water vapor per unit volume of air, expressed in grams of water vapor per cubic meter of air. Specific humidity is the ratio of the density of the water vapor to the density of the air, generally expressed as grams of water vapor per kilogram of air. Specific humidity does not vary with temperature or pressure, since it is a weight-to-weight value, and weight is constant as temperature and/or pressure changes.

RH is the most commonly reported value of humidity. It is expressed as a percentage of actual vapor pressure in the air to the saturation vapor pressure. Since the saturation vapor pressure changes with temperature (Table 7.2), the RH of a parcel of air will change if the temperature changes, even though the absolute amount of water vapor in that parcel remains the same.

For example, if the vapor pressure of a parcel of air at 10°C is 5.0 mmHg, the RH of that parcel is (5.0/9.21) × 100 = 54.3%. If we increase the temperature of the same parcel of air to 15°C without adding or removing water vapor, the RH is (5.0/12.79) × 100 = 39.1%. Thus at 15°C, the air is only 39.1% saturated while at 10°C it is 54.3% saturated. As air heats up, it takes more water molecules to saturate it.

If we know the RH, air temperature, and leaf temperature, we can calculate vapor pressure gradients between leaves and the air to understand water movement. It is useful to understand and compare the movement of water under different situations, for example, water use of leaves of the same plant in the sun versus the shade.

Let's look at a quick example. Suppose we have a generic plant at an air temperature of 20°C and 43% RH, some leaves are in the sun and some of them are in the shade. The leaves in the shade have a temperature of 20°C and the leaves in the sun are 30°C (we'll pretend that we measured the leaf with an infrared thermometer or a thermocouple).

Table 7.2. The saturation vapor pressure (mmHg) of water from −10 to 40°C.

Temperature (°C)	Saturation vapor pressure (mmHg)
−10	2.15
0	4.58
5	6.58
10	9.21
15	12.79
20	17.54
25	23.76
30	31.8
40	55.3

From Table 7.2, the saturation vapor pressure at 20°C is 17.54 mmHg and at 30°C is 31.8 mmHg. If we assume that the RH inside the leaf is nearly 100% and we know that the RH of the air is 43% as defined, we can calculate the vapor pressure of water in: (i) the air; (ii) the leaf in the shade; and (iii) the leaf in the sun.

Atmospheric vapor pressure at 43% RH, 20°C:

$43 = (X/17.54) \times 100$

$0.43 = X/17.54$

$0.43 \times 17.54 = X$

$7.54 = X$

Internal shade leaf vapor pressure at 100% RH, 20°C:

$100 = (X/17.54) \times 100$

$1.00 = X/17.54$

$1.00 \times 17.54 = X$

$17.54 = X$

Internal sun leaf vapor pressure at 100% RH, 30°C:

$100 = (X/31.80) \times 100$

$1.00 = X/31.80$

$1.00 \times 31.80 = X$

$31.80 = X$

Water vapor always moves due to a gradient, from a higher vapor pressure to a lower vapor pressure. We will assume that stomatal resistance and boundary layer resistance to water vapor movement are negligible in this example. Therefore, if you compare the vapor pressure of the leaves and atmosphere you observe:

Shade leaf versus air = 17.54 versus 7.54 = gradient of 10 from leaf to air

Sun leaf versus air = 31.80 versus 7.54 = gradient of 24.26 from leaf to air

Thus in both cases, water vapor will move from the leaf to the air. This is not surprising at all, since we know leaves transpire and water normally moves in this direction. What is interesting is to compare the rate of water vapor movement from shade leaves into the air versus movement from sun leaves into the air:

Sun leaf to air gradient/shade leaf to air gradient = 24.26/10 = 2.426

This number means that leaves in the sun use nearly one and a half times more water than leaves in the shade at the same air temperature and RH! You might have guessed this general result using common sense but may not have known the magnitude of the difference in water use. Now you can prove the magnitude of the difference is as great as it is.

These vapor pressure gradients between internal leaf spaces and the atmosphere are the driving force for transpiration. This is the exit region for water from the plant, so what about the entrance region?

Water in the soil

Soil is a plant's major water source. Soil consists of solid, liquid and gaseous portions, all changing in the percentage of the soil volume they occupy as plants use water and it is replenished or not by precipitation or irrigation. Water in the soil is the primary source of water for plants. Some water can be absorbed by leaves of some species; however, most species absorb water from the soil. The liquid water in the soil is divided into four categories: (i) field capacity; (ii) gravitational water; (iii) capillary water; and (iv) bound water.

Field capacity is the maximum amount of water a soil can hold and only exists immediately after it rains or irrigation has occurred. Water quickly drains (assuming good drainage) from the soil due to the forces of gravity and is appropriately called gravitational water. The water that remains is adsorbed to soil particles creating a thin film around them and is called capillary water. Water that is permanently bound to soil particles and is not available to plants is called bound water. Most of the water available to plants is capillary water, which slowly becomes more difficult to extract from the soil as the soil dries until the point has been reached that all of the capillary water has been used and only bound water remains. As water drains from field capacity through gravitational action, it is available to plants, but generally this water is available for only a short time after saturation.

Water molecules are adsorbed to the soil particles and held in pore spaces, the smaller the pore, the more tightly the water is held. As a soil is depleted of its available water, the remaining water is held more tightly. We are often interested in

knowing how tightly the water is being held in the soil because this gives us an idea of how easily a plant might retrieve it and also often gives us an idea how much water is in the soil.

When all of the available water has been removed from the soil where plants could absorb it, the soil is said to have reached the permanent wilting point. At this point, if soil moisture is not replenished, plants will probably die.

Water is also present in the soil as vapor. The RH of the pore spaces in soil is above 99% even at the permanent wilting point. This water vapor is important for plant growth. Interestingly nearly 85% of the water a seed imbibes during germination in non-saturated soils is water vapor (Wuest, 2007). The idea that seeds need good contact with the soil for good germination is somewhat incorrect. In a soil near field capacity, only 10% of the seed's surface is actually in contact with liquid water. It is more important to ensure that soil moisture losses are minimized during germination by covering the seeds adequately with either soil, mulch or both.

Measuring soil moisture

Soil moisture content can be measured simply by squeezing a handful of soil tightly and observing the ease with which the resulting ball of soil yields to slight pressure. Soils low in water will not form a ball readily and soils high in water content will form a stiff ball which does not readily yield to pressure.

A more reliable method of measuring soil water content is to measure the energy by which water is held by soil particles using a tensiometer. The greater the energy holding the water to the soil particles, the less water there is in the soil available to plants. A tensiometer consists of a porous ceramic tip at the end of a long glass tube with a pressure gauge attached at the top. The porous tip is buried in the soil at a standard depth (10, 20, 40 cm, etc.) and the glass tube is filled with water. A dye is often added to the water to facilitate viewing of the water level in the tensiometer after its tube has been buried in the soil. The pressure gauge is attached to the top of the tube. As water is pulled out of the glass tube through the porous tip in response to decreasing soil moisture, the gauge measures the tension which develops in the tube. Since the porous tip is porous to both water and salts, the osmotic potential of the soil does not

influence readings obtained. Tension is negative and measured in kilopascals (kPa).

We are interested in this energy status (water potential) of water in the soil because water always moves due to a gradient in energy, from a region of high energy to a region of low energy. Just remember that water always moves downhill. The greater the tension, the less available water there is for plants to utilize. Though tension measurements have a negative value, the negative sign is often omitted. If the water potential of the soil as measured by a tensiometer is −12 kPa and a plant root has a water potential of −16 kPa, water would move from the soil into the root. It's not exactly that simple, but it illustrates the need for understanding soil water potential.

Plants and Water Use

Most plants require a tremendous amount of water to survive. This water is needed as a major component of the plant tissues; up to 98% of a plant's fresh weight is water. Water is also needed to maintain a plant's turgor. Without adequate water, plants wilt. Water is also important for cooling leaves via transpiration and evaporation of water from leaves, which removes a tremendous amount of heat energy from the leaf in the process. Water is also a major metabolic player. It is the universal solvent and is involved in many metabolic processes.

The amount of transpiration in a plant varies greatly with species and the environment. As an example, 225 kg of water is used by a single corn plant to produce 1 kg of dry matter. Over its lifetime, a typical plant may use over 100 times its own fresh weight in water. A reasonable estimate of typical transpiration on a leaf area basis is 0.5–2.5 g water/cm^2/h. This translates into as much as 200 l/h for a 'typical' tree. One hectare of corn (*Zea mays*) may transpire as much as 0.6 million l of water in one growing season. This amount of water is equivalent to a 0.4 ha lake, 38 cm deep.

In modern horticulture we need to know how much water a plant needs to maximize quality and quantity of the commodity in question. If we know how much water a plant needs over a defined time frame, we can supply supplemental water via irrigation if needed.

Since exact amounts of water needed for many crops varies by cultivar, location, environmental conditions, soil qualities, etc., a much more useful tool would be one which allows us to estimate how

much water a particular plant or crop needs. Such a tool is an estimate of evapotranspiration, the combined loss of water from the soil via evaporation and transpiration from the plant.

Estimating Water Use by Plants

In order to know how much water is needed from irrigation, we must be able to estimate how much water a crop needs over time and compare that to actual precipitation over the same time period. By using mathematical equations and easily obtained data from local weather stations, we can estimate how much water is used in evapotranspiration and we call our estimate, reference evapotranspiration (RET, formerly called potential evapotranspiration). Simple estimates of RET can be derived from measurements of incoming solar radiation, wind, temperature, and RH. Water use will vary from plant to plant, crop to crop and from day to day. However, these estimates are meant to be calculated daily and summed over time, which provides a fairly good estimate of the amount of water needed.

The ASCE-EWRI Standardized Penman-Monteith equation

The ASCE-EWRI (American Society of Civil Engineers – Environmental and Water Resources Institute) Standardized Penman-Monteith equation is considered the standard equation for estimating the daily evapotranspiration from a crop (Monteith, 1965; Allen *et al*., 1998).

$$ET_{sz} = \frac{(0.408\,\Delta(R_n - G) + \lambda \dfrac{C_n}{T + 273} U_2(e_s^o - e_s)}{\Delta + \lambda(1 + C_d U_2)}$$

Where:
ET_{sz} = the standardized evapotranspiration for a short (ET_{os}) or tall (ET_{rs}) reference crop in millimeters per day (mm/day)
Δ = the slope of the vapor pressure curve [kPa/°C]
R_n = net radiation at the crop surface [MJ/m^2/day]
G = soil heat flux density [MJ/m^2/day]

λ = latent heat of vaporization of water = 2.45 MJ/kg (which is a psychrometric constant)
C_n and C_d are reference values for specific crops: Cn = 900 and 1600 for short or tall crops, respectively, and Cd = 0.34 or 0.38 for short or tall crops, respectively.
T = mean air temperature in °C
U_2 = wind speed in meters per second (m/s) at 2 m above the ground
e_s^o = the saturation vapor pressure of water at T
e_a = the actual vapor pressure of water at T, derived from RH

Let's examine the calculations needed in order to estimate evapotranspiration from the following weather data: average daily (24 h average) values for solar radiation, wind, temperature, and RH. We will examine the calculations as we walk through the equation to see where we can derive the pieces of information needed to complete our estimate. Where possible, variables that can be generalized to a constant value for most locations and conditions will be utilized for our discussion. Those who wish to use a more rigorous approach with more calculations are encouraged to check the references.

$$ET_{sz} = \frac{(0.408\,\Delta(R_n - G) + \lambda \dfrac{C_n}{T + 273} U_2(e_s^o - e_a)}{\Delta + \lambda(1 + C_d U_2)} \qquad \text{[AU 1]}$$

Let's assume λ = 0.067 for an altitude of 0 m (sea level), making our equation:
(See equation (1) at bottom of page).

The value of Δ

We need to know the value of Δ which we can derive from the formula: [AU 1]

$$\Delta = \frac{4098\left[0.6018\,exp\left(\dfrac{17.27T}{T + 237.3}\right)\right]}{(T + 237.2)^2}$$

Where:
Δ = slope of saturation vapour pressure curve at air temperature T [kPa/°C]

$$ET_{sz} = \frac{(0.408\,\Delta(R_n - G) + 0.067\,\dfrac{C_n}{T + 273} U_2(e_s^o - e_a)}{\Delta + 0.067\,(1 + C_d U_2)} \qquad\qquad (1) \quad \text{[AU 1]}$$

T = air temperature [°C]
exp[..] = 2.7183 (base of natural logarithm) raised to the power [..]

R_n: Net solar radiation at crop level

Let's take a look at R_n, the net radiation at the crop surface [MJ/m²/day], which normally turns out to be positive except under extreme conditions. R_n is the difference between the incoming net shortwave radiation (R_{ns}) and the outgoing net longwave radiation (R_{nl}):

$$R_n = R_{ns} - R_{nl}$$

We need estimates for R_{ns} and R_{nl}.

R_{ns} is the net shortwave radiation resulting from a balance between incoming and reflected radiation, given by the equation:

$$R_{ns} = (1 - \alpha)\, R_s$$

Where:
R_{ns} = net solar or shortwave radiation [MJ/m²/day]
α = albedo or canopy reflection coefficient, which is often estimated as 0.23
R_s = the incoming solar radiation [MJ/m²/day]
   To complete the above calculation, we need an estimate of R_s. We can get that from the following formula:

$$R_s = \left(0.25 + 0.75\frac{n}{N}\right)R_a$$

Where:
R_s = solar or shortwave radiation [MJ/m²/day]
n = actual duration of sunshine in hours [h]
N = maximum possible duration of sunshine or daylight hours [h], calculated as:

$$N = \frac{24}{\pi}\omega_s$$

Where:
ω_s = sunset hour angle [rad], which is:

$$\omega_s = arccos\, [-\tan(\varphi)\,\tan(\delta)]$$

φ = latitude [rad], which is:

$$[\text{Radians}] = \frac{\pi}{180}[\text{decimal degrees}]$$

R_a = extraterrestrial radiation [MJ/m²/day]
But we need to know R_a in order to finish the previous equation. We can calculate R_a from the following formula:

$$R_a = \frac{24(60)}{\pi}G_{sc}d_r[\omega_s sin_\varphi sin_\delta + cos_\varphi cos_\delta sin_{\omega s}]$$

Where:
R_a = extraterrestrial radiation [MJ/m²/day]
G_{sc} = solar constant = 0.0820 MJ/m²/min
d_r = inverse relative distance earth–sun, which is:

$$d_r = 1 + 0.033 cos\left(\frac{2\pi}{365}J\right)$$

Where:
J = Julian date
ω_s = sunset hour angle [rad], which is:

$$\omega_s = arccos\, [-\tan(\varphi)\,\tan(\delta)]$$

φ = latitude [rad], which is:

$$[\text{Radians}] = \frac{\pi}{180}[\text{decimal degree}]$$

If you know your latitude in degrees and minutes, convert it to decimal degrees by the formula:

$$\text{decimal degree} = \text{degree} + \frac{\text{min}}{60}$$

δ = solar declination [rad], which is:

$$\delta = 0.409 sin\left(\frac{2\pi}{365}J - 1.39\right)$$

Where:
J = Julian date
An example:
What is the extraterrestrial radiation (R_a) for a location 20°S latitude on 3 September?

$$R_a = \frac{24(60)}{\pi}G_{sc}d_r[\omega_s sin_\varphi sin_\delta + cos_\varphi cos_\delta sin_{\omega s}]$$

G_{sc} = solar constant = 0.0820 MJ/m²/min
(See equation (1) at bottom of page).

$$R_a = \frac{24(60)}{\pi}\,(0.0820)\,d_r[\omega_s sin_\varphi sin_\delta + cos_\varphi cos_\delta sin_{\omega s}] \tag{1}$$

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d_r = inverse relative distance earth–sun, which is:

$$d_r = 1 + 0.033 cos\left(\frac{2\pi}{365}J\right)$$

Where: J = Julian date = 246

$$d_r = 1 + 0.033 cos\left(\frac{2\pi}{365}246\right)$$

$$d_r = 0.985$$

ω_s = sunset hour angle [rad], which is:

$$\omega_s = arccos\ [-tan\ (\varphi)\ tan\ (\delta)]$$
$$\omega_s = 1.527$$

φ = latitude [rad], which is:

$$[Radians] = \frac{\pi}{180}[decimal\ degrees]$$

$$[Radians] = \frac{\pi}{180}[-20] = -0.35$$

δ = solar declination [rad], which is:

$$\delta = 0.409 sin\left(\frac{2\pi}{365}J - 1.39\right)$$

$$\delta = 0.409 sin\left(\frac{2\pi}{365}246 - 1.39\right)$$

$$\delta = 0.120$$

Thus:

(See equation (1) at bottom of page).

Now we can calculate R_s:

$$R_s = \left(0.25 + 0.75\frac{12}{12}\right)R_a$$
$$R_s = (1)32.2$$
$$R_s = 32.2\,MJ/m^2/day$$

This calculation assumed a mostly sunny day where the total number of sunlight hours (n) was 12 and the total possible number of sunlight hours (N) was 12.

$$R_{ns} = (1 - \alpha)R_s$$

$$R_{ns} = (1 - 0.23)32.2$$

$$R_{ns} = (0.77)23.2$$

$$R_{ns} = 24.794$$

Remember, we are ultimately trying to calculate $R_n = R_{ns} - R_{nl}$, so we need an estimate of R_{nl}.

R_{nl}: Net longwave radiation

(See equation (2) at bottom of page).
Where:
R_{nl} = net outgoing longwave radiation [MJ/m²/day]
σ = Stefan-Boltzmann constant [4.903 10⁻⁹ MJ/K⁴/m²/day]
$T_{max,K}$ = maximum absolute temperature during the 24 h period [K = °C + 273.16]
$T_{min,K}$ = minimum absolute temperature during the 24 h period [K = °C + 273.16]
e_a = actual vapour pressure [kPa]
R_s/R_{so} = relative shortwave radiation (limited to ≤ 1.0)
R_s = measured or calculated solar radiation [MJ/m²/day]
R_{so} = clear-sky radiation [MJ/m²/day] calculated as:

$$R_{so} = (0.75 + 0.00002z)R_a$$

Where:
z = elevation above sea level (m)
For our example, the minimum and maximum temperature for the day were 21°C and 27°C, the elevation is 0 m (we're at sea level) and the actual vapor pressure was 2.1 kPa:

$$R_{nl} = 0.000004903\left[\frac{300.16^4 + 294.16^4}{2}\right]$$

$$\left(0.34 - 0.14\sqrt{2.1}\right)\left[1.35\frac{32.2}{24.15} - 0.35\right]$$

$$R_a = \frac{24(60)}{\pi}(0.0820)(0.985)[1.527(-0.041) + 0.93 sin(1.527)] \tag{1}$$
$$R_a = 32.2\,MJ/M^2/day$$

$$R_{nl} = \sigma\left[\frac{T_{max,K}^4 + T_{min,K}^4}{2}\right]\left(0.34 - 0.14\sqrt{e_a}\right)\left[1.35\frac{R_s}{R_{so}} - 0.35\right] \tag{2}$$

$$R_{nl} = ?$$

So now we can calculate:

$$R_n = R_{ns} - R_{nl}$$

$$R_n = 24.794 - ?$$

Soil heat flux (G)

$$G = c_s \frac{T_i + T_{i-1}}{\Delta t} \Delta z$$

Where:
G = soil heat flux [MJ/m²/day]
c_s = soil heat capacity [MJ/m³/°C]
T_i = air temperature at time i [°C]
T_{i-1} = air temperature at time i–1 [°C]
Δt = length of time interval [day]
[AU 1] Δz = effective soil depth [m]

However, when values are calculated daily, G can be ignored, since the soil heat flux is going to be very, very small and thus is close to 0.

Wind speed

Wind speed is accurately measured with an anemometer in meters per second and expressed as: U_2 = m/s, measured 2 m above the ground.

e_s – e_a: The vapor pressure defecit

If we know the RH we can calculate e_a. Since RH varies over the day, we need an average RH value for the day (less desirable) or an average e_a value derived from RH_{max} and RH_{min} values for the day (more desirable). We must first retrieve values of e_s^o from a reference book, or we can calculate it if we know the air temperature using the following formula:

$$e_s^o = 0.6108 exp \left[\frac{17.27T}{T + 237.3} \right]$$

Where:
e_s^o = saturation vapor pressure at the air temperature T [kPa]
T = air temperature [°C]
$exp[..]$ = 2.7183 (base of natural logarithm) raised to the power [..]

Remember to calculate an e_s^o value for both the T_{max} and T_{min}.
Now if we know $e_{s\,min}^o$, $e_{s\,max}^o$, RH_{max} and RH_{min}, we can calculate e_a from the formula:

$$e_a = \frac{e_s^o (T_{min}) \frac{RH_{max}}{100} + e_s^o (T_{max}) \frac{RH_{min}}{100}}{2}$$

From all of this, we want to calculate a vapor pressure deficit using the following formula:

$$e_s - e_a = \left[\frac{e_s^o (T_{max}) + e_s^o (T_{min})}{2} \right] - e_a$$

Estimated evapotranspiration

We now have all the information we would need to calculate an estimate of the evapotranspiration that would occur in 1 day.

$$ET_{sz} = \frac{(0.408\Delta\,(R_n - G) + \lambda \dfrac{C_n}{T + 273} U_2 (e_s^o - e_a)}{\Delta + \lambda\,(1 + C_d U_2)}$$

Where:
Δ = the slope of the vapor pressure curve [kPa/°C]
R_n = net radiation at the crop surface [MJ/m²/day]
G = soil heat flux density [MJ/m²/day]
λ = latent heat of vaporization of water = 2.45 MJ/kg (which is a psychrometric constant)
C_n = 1600
C_d = 0.38
T = mean air temperature in °C
U_2 = wind speed in meters per second (m/s) at 2 m above the ground
e_s^o = the saturation vapor pressure of water at T
e_a = the actual vapor pressure of water at T, derived from RH

With careful calculations and a bit of work, one can estimate the general water requirements for a crop and monitor precipitation to determine when, and if, and how much supplemental moisture is needed. For an excellent step-by-step walk through an example please visit http://edis.ifas.ufl.edu/ae459 or refer to Zotarelli *et al.* (2010).

Transpiration – Water Potential and Water Movement in Plants

Transpiration is especially important for cooling plant leaves, particularly those exposed to direct incoming solar radiation. It is also important for transporting nutrients from the soil to growing leaves and meristems and for providing water for the mass flow of nutrients from sources of photosynthates (leaves) to sinks (fruits, roots, meristems).

The driving force of transpiration is the difference in water potential between two components in the transpiration stream, such as soil to root, root to stem, stem to leaf, and leaf to air. Water potential is one of those concepts in plant physiology that many find difficult to comprehend, probably because they make it more difficult than it really is.

Water potential in plants: $\psi = \psi_{osm} + \psi_{pres}$

Water potential in plants consists of two major components, osmotic potential and pressure potential. Osmotic potential is that part of water potential regulated by the presence of molecules other than water in a solution. Those other molecules might include proteins, sugars or salts. Pressure potential is that component of water potential due to the increase in pressure within a cell due to the presence of a cell wall or the tension (negative pressure) generated by the pull of water molecules along the transpiration stream.

We indicate water potential symbolically as ψ. We indicate the osmotic component as ψ_{osm} and the pressure component as ψ_{pres}. Collectively they provide the following equation to describe water potential:

$$\psi = \psi_{osm} + \psi_{pres}$$

So what is the unit of measure? Osmotic potential and its components are measured in megapascals (MPa). Most of the time ψ_{osm} is negative (we'll see why shortly), ψ_{pres} is positive (unless under tension in the xylem where it would be negative) and the two components added together usually give ψ a negative value. Just how negative ψ is comparing one part of the transpiration stream to another determines the direction of water flow in the system.

In order to understand how the components of ψ influence water movement in the plant system, the energy concept surrounding ψ must make sense. A measure of molecular energy called Gibbs free energy is defined for pure water to be equal to 0.0. This free energy is the energy we call ψ. With this in mind, consider a container of pure water with molecules bouncing around inside the container. The energy contained in their bouncing around is the Gibbs free energy and is equal to 0.0. It seems a little strange that bouncing molecules have an energy value of 0.0, but that's the way it is.

If we now add some molecules of a solute such as glucose, sodium chloride, or a water-soluble protein, these solute molecules are going to interfere with the movement of the water molecules and slow them down. The free energy of the water molecules will be less than what it was with no solute, thus it will be negative. We would then say that the osmotic portion (ψ_{osm}) of ψ is <0.0. With no lid on the container, ψ_{pres} would remain 0.0. Thus $\psi = \psi_{osm} + \psi_{pres}$ will be negative. The more solvent added to the water, the more molecules interfere with water molecule movement, thus the more negative ψ_{osm} will be.

The ψ gradient

The same general scenario occurs in a plant cell except for the pressure potential. Since the cell is surrounded by a cell wall, pressure can build up and ψ_{pres} will be >0.0. In many instances, $\psi_{pres} < \psi_{osm}$, so ψ <0.0. In some cells, such as xylem cells, tension (ψ_{pres} <0.0) can develop which causes ψ to be very negative.

Water molecules move due to the gradient in ψ, moving from an area of higher (more positive) ψ to an area of lower (more negative) ψ. Water always moves downhill. The solute molecules may or may not move with the water, depending on barriers, such as cell walls and plasma membranes that separate the two regions in question.

Consider the general path of water movement from the soil through the plant into the atmosphere. Each component of the path has a ψ value depending on solutes and barriers which might generate pressure. Water will move along the pathway in response to differences in ψ. Table 7.3 includes hypothetical values for components in the pathway of water movement in a typical plant. Most living plant cells have an osmotic potential ranging from –0.5 to –1.2 MPa but may be as high as –2.5 MPa in cells storing a large amount of sucrose. Intercellular spaces in many roots and stems are typically around –0.1 MPa. Larger intercellular spaces in leaves may often reach –8.0 MPa. Pressure potential in typical cells ranges from 0.1 to 1 MPa but can be negative (about –1.0 MPa) in xylem cells. Typical soil solutions have a water potential between –0.1 MPa (soil at field capacity, low solute levels) to –2.0 MPa (significant water stress). During a drought, soils may reach a water potential of –2.5 MPa.

Looking at the values of ψ in Table 7.3, it is fairly easy to understand the movement of water through a plant due to differences in ψ. But there are other important forces at work which contribute to the mechanisms of transpiration.

Table 7.3. Hypothetical values of water potential ψ for various components in the path of water movement in a typical plant.

Component	ψ MPa
Soil solution	–2.0
Root epidermal cell	–0.025
Root endodermal cell	–0.1
Root xylem cell	–0.4
Stem xylem cell	–0.8
Leaf xylem cell	–1.2
Leaf mesophyll cell	–1.7
Intercellular space in leaf mesophyll	–8.0
Atmosphere surrounding leaf (20°C, 40% RH)	–100.0

ψ At the cellular level

The fact that a cell has a cell wall affects ψ tremendously by its influence on ψ_{pres}. Consider a flaccid root epidermal cell. There is a certain amount of solute in it and it will eventually fill a finite volume once it absorbs water. If we assume the number of solute molecules is not going to change all that much, we can assume that water will flow into the cell from the outside, thereby changing the concentration of molecules and ψ by changing ψ_{osm}. Once the volume is occupied, ψ will change due to changes in ψ_{pres} rather than ψ_{osm}. Once the volume of the cell is filled with water, not many water molecules can continue to enter, but each one that does, increases the pressure a great deal.

Equilibrium is often discussed when studying water movement in response to differences in ψ. However, equilibrium is never really reached since organisms usually exist in a system of gradients rather than any type of equilibrium. The gradients allow for the flow of the components of life among cells, tissue, organs and their respective environments.

Two adjacent cells will exchange water based on the difference in ψ between the two cells. Water will move from the cell with the more positive value of ψ to the cell with the more negative ψ. This movement will continue until the two cells have the same ψ. We might be tempted to say they are now at equilibrium. But even though ψ may be at equilibrium, this equilibrium was reached by changes in the ψ, and probably changes in the concentration of sucrose, sodium chloride, soluble proteins, etc. These concentrations are not in equilibrium, and since the plasma membrane is permeable, molecules of these

solutes are likely to move across the membranes, altering each cell's ψ, causing water molecules to move, which causes changes in solute concentration, etc. So see how equilibrium is never really reached?

ψ Across the root

Let's take this discussion even further. Consider the movement of water from the soil across a typical root to the xylem for transport to the leaves. To reach the xylem cells, water has to traverse the root epidermis, the cortex, the endodermis, and finally the xylem cell wall. Water moves across the root symplastically from the cytoplasm of one cell to the cytoplasm of an adjacent cell. As long as cells remain intact, there are no barriers to symplastic movement of water in plant roots. Water may also move apoplastically across the root, remaining outside of the cytoplasm, moving through intercellular spaces and cell walls. There is a barrier to water movement through the apoplast in a root and it is called the endodermis. It is a ring of suberized cell walls (casparian strips) surrounding the vascular cylinder, preventing apoplastic movement of materials into the xylem. In order for water or any solute to move into the xylem, it must do so symplastically. Since the plasmalemma is selectively permeable, some solutes can pass through while others cannot. The endodermis creates a barrier which helps regulate the movement of solutes into the xylem for transport to other regions of the plant.

A gradient in ψ_{osm} is maintained from the vascular cylinder across the root to the epidermis by a concomitant gradient in sucrose delivered from the leaves through the phloem. As sucrose diffuses into cells it can: (i) remain in solution affecting ψ_{osm}; (ii) be metabolized for root cellular processes; or (iii) it can be stored as starch which does not affect ψ_{osm} (starch is not soluble in water).

In addition, a gradient in ψ_{pres} exists across the root, and we should pay particular attention to the negative ψ_{pres} (or tension) which exists in xylem cells. This negative ψ_{pres} helps pull water into the xylem cells for transport to the leaves. This pull is made possible by water's cohesive properties. Cohesion is an attraction of like molecules, such as water for water, which keeps them held together tightly. Thus they in effect pull each other along. Another property of water, adhesion, is the attraction of water molecules for negatively charged surfaces. Glass is a good example of a negatively charged
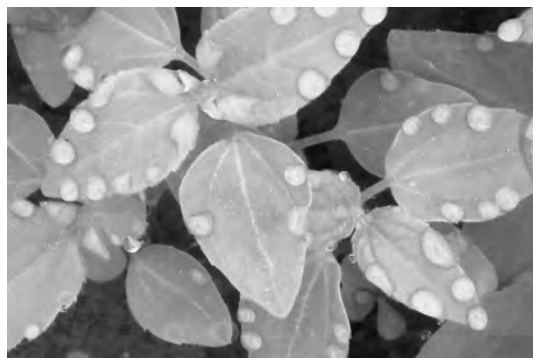
surface. The xylem cell wall is also negatively charged. Thus water molecules are attracted to the xylem cell wall and to each other. These combined properties allow for capillary movement in water through the xylem vessels.

So we've moved the water from the soil across the root and into the xylem. Most of the water absorption in roots takes place in the root tissue just behind the root tip and the zone of elongation. The epidermis of older root tissue is usually too suberized to allow water entry.

The accumulation of minerals due to active transport across the endodermis into the vascular cylinder (stele) creates a rather negative ψ_{osm} which results in water movement into the stele. Under periods of low transpiration (night time, cloudy, cool weather) pressure may build up in the stele forcing water up through the xylem, often exiting the leaf via hydathodes, specialized structures at the margins of the leaves (Fig. 7.2). Droplets of xylem sap may appear along the leaf margin at the hydathodes. This is called guttation.

ψ Up the stem

Water movement up the xylem is possible due to capillarity of the xylem–water system, and the cohesive and adhesive properties of water. In order for the water to be pulled through the xylem, a continuous column of water must exist from the root through to the leaf. If this column breaks, it is called cavitation. Ultimately this break may repair itself and transpiration can continue. (Remember you have hundreds or

thousands of these continuous xylem vessels in a given plant, thus if some of them cavitate, it's not the end of the world.) Some species have regulatory pits in xylem cells called bordered pits which can control the changes in pressure (tension) which causes cavitation, by controlling water movement in and out of the cell through the pits. Cavitation is then prevented for the most part.

The ultimate driving force for transpiration is the evaporation of water from the leaf. This is accomplished by the tremendous gradient of water potential from the leaf (–2 KPa) to the atmosphere (–100 KPa, 20°C, 50% RH). Liquid water bathes the cell walls of mesophyll cells inside the leaf, causing the water content of the intercellular spaces in the leaf to be at or near saturation. Water vapor then moves out of the leaf through the stomata where it evaporates into the atmosphere. This evaporation is the force which initiates the pull of water up through the xylem from the soil.

Environmental Factors Affecting Transpiration

The rate of transpiration in plants varies considerably among species and is affected by many environmental factors, especially light, temperature, RH, wind, and water (Fig. 7.3).
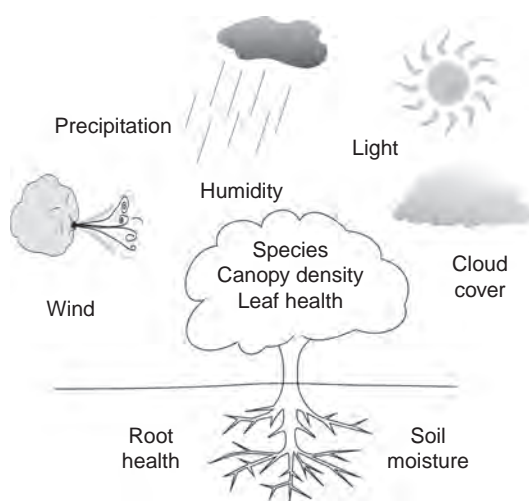
Fig. 7.3. Factors affecting transpiration. (Cloud, wind, precipitation and sun symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science, ian. umces.edu/symbols/.)

Fig. 7.2. Guttation visible on leaf margins of kale (*Brassica oleracea*, Acephala Group) 'Red Russian' early in the morning.

Light

Light regulates transpiration directly through effects on: (i) stomatal opening and closing; (ii) photosynthetic rate; and (iii) leaf temperature.

Stomata open and close in response to K^+ ions moving into and out of the guard cells and concomitant influxes and outfluxes of water. Blue light is absorbed by the pigment phototropin which activates a proton pump, driven by ATP from photosynthesis, which pumps H^+ ions out of guard cells. As protons are pumped out of the guard cells, K^+ enter the guard cells to relieve the increasing negative charge which develops in the guard cell due to H^+ leaving. This makes the ψ more negative, causing water to enter guard cells, increasing turgor and causing the stomata to open.

If soil water is not sufficient to keep up with transpiration requirements, the stomata must close. In most higher plants, abscisic acid (ABA) triggers stomatal closing. This often occurs around mid-day on a hot summer day. How does ABA do it? ABA binds to receptors on the surface of guard-cell plasma membranes which causes an increase in cytosolic pH and a transfer of Ca^{2+} from the vacuole to the cytosol. This stimulates a loss of anions, especially $NO3^-$ and Cl^-, as well as K^+ from the cell which reduces ψ and leads to a loss of turgor. The guard cells become flaccid and the stomata close.

Temperature

Transpiration increases with temperature for several reasons. Water evaporates faster at warmer temperatures. Additionally, metabolism increases (up to a point) with temperature, thus metabolic demands for water increase with temperature. In addition, when the temperature of a parcel of air increases, its RH decreases. This thereby increases the leaf-to-atmosphere water gradient, increasing transpiration.

Humidity

Transpiration increases with decreased RH. As the RH of the air decreases, the water vapor gradient between the leaf and the atmosphere increases, increasing the rate of transpiration. Even at 90% RH, the ψ of the atmosphere is much more negative (−14 KPa, 20°C) than the ψ of any leaf under any condition.

Wind

Wind primarily affects transpiration by influencing the depth of the boundary layer between a leaf and the atmosphere. The thin layer of air surrounding a leaf is called the boundary layer. The humidity of this boundary layer is nearly 100%, thus the thicker the boundary layer, the lower the rate of transpiration. On a calm day with little or no wind, this boundary layer can become relatively thick. On a windy day, this layer of moist air is constantly being swept away, thereby increasing transpiration.

Wind may also cool the leaf, resulting in reduced transpiration. Additionally, if it is windy enough, stomata may close, reducing transpiration.

Soil water

Two attributes of soil moisture affect transpiration. First, when water is plentiful in the soil, ψ will increase allowing more water to enter the root more quickly. As the soil dries, water is held more tightly by soil particles, decreasing ψ, making it more difficult for water to enter the root. The quality of the soil water also influences transpiration. If the soil water is salty due to natural reasons or excessive fertilizer applications, the ψ of the soil water will be more negative, regardless of the amount of water present, and this will make it more difficult for plants to access water, thus reducing transpiration.

Plant adaptations affecting transpiration

Many plant factors influence how adapted a plant is to reduced water availability. Some of these attributes may change as a plant develops throughout the growing season, others are genetically predetermined.

Larger leaves generally transpire more than smaller leaves. Leaf size may decrease as water stress occurs, reducing transpiration. Some plants adapted to regions with low available soil moisture inherently have small leaves.

Plants with a greater number of leaves tend to transpire more than those with fewer leaves. One major response of plants to water stress in an attempt to reduce transpiration and conserve water is a reduction in the number of leaves per plant via premature abscission. Wilting of leaves due to lack of turgor, reduces exposure to radiant energy,

thereby cooling the leaf somewhat and reducing photosynthesis and transpiration.

The number, distribution, and position of stomata greatly influence transpiration rate. Most stomata are on the underside of the leaf (abaxial). Fewer stomata per unit leaf area usually translate to reduced transpiration rates. Stomata may also be sunken, creating a miniature boundary layer immediately surrounding the sunken stomata which greatly reduces transpiration.

The cuticle thickness of a leaf influences the rate of transpiration. The cuticle is a waxy layer on all above-ground plant tissue which helps prevent direct water loss through epidermal cells. With a waxy covering in place, water is forced to move through the transpiration stream and out through the stomata. Thicker leaf cuticles reduce transpiration. Generally, plants from hot climates have a thicker cuticle than those from a cooler climate. Leaves growing in the sun also have a tendency to have thicker cuticles than those growing in the shade.

Leaf pubescence (hairiness) can alter transpiration. Epidermal hairs increase the boundary layer of a leaf, thereby reducing transpiration.

Antitranspirants

Antitranspirants are chemicals sprayed on plant leaves in an attempt to reduce water use by reducing transpiration. They act by either closing the stomata or coating leaves and clogging stomata to reduce transpiration. In general, the use of antitranspirants is not recommended as a common horticultural practice.

One exception to this rule is the use of an antitranspirant on evergreen species during the winter if they are exposed to harsh, drying winds and frozen soil. Frozen soil prevents water absorption and can even draw water out of the roots while the drying winds disturbs the boundary layer around leaves or needles, causing excessive water loss. In this situation, an antitranspirant may be of value for reducing loss from desiccation.

Plant Growth and Water Supply

Most plants require a steady supply of water during their growth and development for maximum production and best quality. Any interruption in the water supply will likely reduce final yields and crop quality. There are several crucial periods when lack of water can be extremely detrimental to production.

Any interruption of the water supply during germination could lead to death of the seedling. Roots are not usually extensively developed in the soil profile as the seedling germinates which makes a reliable water supply crucial. Later in the plant's development, roots may be developed enough to obtain water from deeper in the soil.

Rapid, early vegetative development is often necessary in many crops to establish a good plant framework on which to produce the crop. If vegetative growth is stunted, yields will likely be reduced. Once a good framework has been established, the next crucial stage is flowering.

Any water stress during flowering is likely to inhibit pollination and/or fertilization leading to flower abscission and lack of fruit. Stress after fertilization could lead to embryo abortion, and in most cases premature fruit abscission, greatly reducing yield.

In many fruit crops, water is crucial to the final stage of fruit development. That stage, final fruit swell, is a period of rapid and extensive cell enlargement. Any water stress reduces cell enlargement reducing final fruit size (an important economic consideration in many crops) and yield.

While water stress is usually detrimental to plant growth and development, there are times when stress from lack of water might lead to positive outcomes. In some crops, flowering or flower bud formation may be induced by lack of water. In protected culture of low-chill blueberries, water stress can substitute for the chilling required to break endodormancy. It is much easier to carefully induce water stress than to supply artificial chilling to plants in order to break dormancy and initiate out-of-season production.

Late-season irrigation should be monitored so that it does not induce growth. Late-season growth is often less cold hardy than early and mid-season growth. Slight water stress late in the growing season can sometimes increase the cold hardiness of some perennial species.

Irrigation – Supplying Extra Water

Agricultural irrigation is the number one use of water on a global scale. Water is becoming an increasingly precious commodity and effective management in horticultural production systems is imperative. As food for thought (no pun intended) it requires 2400 l of water to produce one average

hamburger, 200 l to produce one glass of milk, 135 l for one egg, 70 l for an apple, 40 l for a slice of bread, and 25 l for one average potato (FAO, 2011). Keep this in mind the next time you turn on the faucet (tap), go to the well, or fire up your irrigation pump.

The simplest irrigation system is a watering can or a garden hose with a sprinkler attachment. Most production systems, however, require a more elaborate set up. The major types of irrigation systems include ditch, overhead, or trickle, with their water source being groundwater, surface water, or a municipal water supply.

When considering a water source for irrigation, several components of irrigation must be considered: (i) water quantity needed; (ii) water sources and supply rate; and (iii) water quality.

Irrigation water

Water quantity

Any irrigation system must be able to supply a crop's water needs that are not met by the expected effective rainfall. Effective rainfall is that precipitation that falls and is readily absorbed by the soil. Ineffective rainfall is that rainfall that runs off due to intensity of precipitation or topography. In addition to the total amount needed over the growing season, consideration must be given for daily needs which will change over the crop's course of development. Water use is most often measured as: (i) inches of rainfall (or irrigation); (ii) acre-inches (1 acre-inch is 1 inch of water applied to 1 acre); or (iii) gallons per minute (Gpm).

As an example, let's determine the water needs of a 100 acre vegetable farm. Suppose the farm has a peak use rate of 0.25 inches/day (this estimate can be obtained from a local agriculture expert). The farm would require 100 acres × 0.25 inches = 25 acre-inches/day. Most growers do not run irrigation systems 24 h a day, so suppose you calculate that you will run it for only 16 h a day. This would indicate a water use rate of 25 acre-inches ÷ 16 h = 1.56 acre-inches/h. As 1 acre-inch/h equals roughly 453 gallons/min, therefore, 1.56 acre-inches/h × 453 = 708 Gpm. No irrigation system is 100% efficient at delivering the water to the crop, therefore, this number of 708 must be adjusted to consider the efficiency rating of the system in question (Table 7.4).

Table 7.4. Water system efficiencies for several types of irrigation.

Irrigation system	Minimal efficiency (%)
Surface – basin	80
Surface – border strip	70
Surface – furrow	60
Sprinkler – portable	65
Sprinkler – traveling gun	60
Sprinkler – center pivot, linear move	75
Sprinkler – permanent	70
Trickle – point source emitters	75
Trickle – line source	70

If you were using trickle tape, for example, your source must be able to supply a minimum of 708/0.70 (70% minimum efficiency for line source trickle) = 1011 Gpm.

Water source

One of the first things to consider when selecting your water source from those available in your area, is whether or not you have the legal right to that water. Additionally, you must ensure that you have the right to draw the quantity needed, when you need it. If you must drill a well, make sure you have the right to do so.

Water sources include: (i) rivers and streams; (ii) lakes, ponds, and reservoirs; and (iii) wells. Rivers and streams often have variable flow rates depending on season and precipitation patterns. If natural rainfall is in short supply, river and stream flow is also likely to be reduced. If you have the right to the river or stream water and the flow is variable, you will probably require an on-farm storage facility. Lakes, ponds or reservoirs are good sources of irrigation water if you have the legal right to tap into them and the water flow into them is adequate. If none of these sources are applicable to your situation, you may need a well. Deep-drilled wells are usually most reliable for irrigation purposes. Again, you must make sure you have the right to drill a well.

Municipal water may be an expensive alternative. Additionally, consider that most sewer bills are calculated from water bills, so you'll be paying for sewage removal you are not using!

Once you establish your source of water, you must make sure you can get the water to your fields effectively. Consider distance, elevation, terrain, etc. The farther you are from the source, the more

pumping power you'll need. Pumps use electricity or diesel fuel, thus they are expensive to operate. Sometimes it's less expensive to select a different source (i.e. drill a well) than to pump water over a long distance.

Water quality

Water quality may not be consistent over the growing season, thus it is important to examine possible changes to water quality over time. Not only should natural changes be considered, but human-induced changes must also be examined. It is always a good idea to have your water tested often for natural and introduced contaminants. This includes testing for salts, industrial wastes, organic acids and bacteria from decaying plant or animal waste material.

Other contaminants you should consider include sand, silt, clay, and algae, particularly with trickle systems, as they are easily clogged. Filters are normally needed for trickle systems.

Irrigation systems

Selecting an irrigation system

Selecting an irrigation system should be a major part of the farm planning process. In planning the system, it is important to consider a number of issues.

Physical characteristics of the environment which may affect the operation and efficiency of an irrigation system are important. The soil is extremely important in selecting a system. Its texture, depth, and uniformity will affect infiltration capacity and rate, and drainage. Its initial salinity level sets the level for how much additional salt can be applied via irrigation water before substantial problems arise. Site characteristics such as topography indicate potential erosion issues. The crops which will be grown and the growing climate have a large impact on system selection. If crops will need frost protection utilizing the irrigation system, this must be incorporated into the decision. The source of the water must be considered. Is it high quality or does it have contamination issues with salts, other chemicals, or particulate matter? Is the water easy to get to and relatively close to the area of crop production? Is it a reliable source? If the system under consideration requires energy, is it readily available, reliable, and at a reasonable cost?

After determining if an irrigation system is feasible, economics of purchase, use, and maintenance must be studied. Most systems require a substantial initial investment of time and money. Once purchased and installed, time and money must be allocated for operation and maintenance.

If the site and economics are suitable, consideration must be given to legal and social issues. Permits must be obtained and the surrounding community must be favorable to the presence of the irrigation system. Is there potential for vandalism in the neighborhood? Labor with enough skill must be available for operation and maintenance of the system.

SURFACE IRRIGATION SYSTEMS

BASIN IRRIGATION Basin irrigation utilizes application of water to a completely level area surrounded by raised borders. The size of an area that can be irrigated with this system is limited by the amount of water available for one irrigation cycle. This type of system works well with large, level land parcels with uniform well-drained soil where adequate water is available. It is a fairly simple system with low labor requirements.

BORDER STRIP IRRIGATION Border strip irrigation incorporates land formed into strips that are level across the narrow dimension but slightly sloped in the long dimension and surrounded by a border. Water enters the field on the upper end of the border and flows down the sloped strips. While simple in conception, this is a very complicated system to manage.

While border length and slope are easily set, other factors entering the system such as moisture deficit at the time of water application, infiltration rate, and flow interference by the crop makes the system tricky to run.

FURROW IRRIGATION Furrow irrigation consists of furrows sloping down the length of a field to which water is applied. Water infiltrates vertically and horizontally. Many designs are possible with this method of irrigation. With good planning and management, this system can be quite effective. However, mismanagement can lead to undesirable results very quickly.

SPRINKLER IRRIGATION Sprinkler irrigation delivers water through a pressurized network to sprinklers, jets or nozzles which spray water into the air, creating

artificial rain. The basic components of this type of system are: (i) a water source; (ii) pump; (iii) piping network; (iv) control valves; and (v) sprinklers.

PORTABLE SPRINKLER IRRIGATION   This type of system consists of a main supply line with lateral pipes to which the sprinklers are attached at regular intervals. The pipe is often lightweight aluminum 6–12 m (20–40 feet) in length with quick-connect joints for easy assembly and disassembly. Sprinklers are attached directly to the lateral pipe, or are on tall risers to raise them above the crop being irrigated, or on short risers to keep them below the crop canopy, as in orchards. Ordinarily one section of the field is irrigated at a time. The pipes must then be moved, and the next section irrigated. The initial cost of such a system is often low; however, labor costs for moving pipes can be high.

SIDE ROLL   This is essentially a portable system mounted on wheels, with the lateral line serving as the axle. The wheels are high enough so that the lateral pipe clears the crop being irrigated. The wheels move via a gasoline-powered engine. The entire unit moves from one position to another for irrigating, rather than requiring constant disassembly and assembly.

TRAVELING GUN   The travelling gun is a high-pressure sprinkler gun mounted on a trailer. Water is supplied via a flexible hose. The gun is moved to the far end of the field and water pressure operates a conveyor system which pulls the irrigating gun through the field by winding the supply hose onto a large wheel on the close side of the field.

CENTER PIVOT AND LINEAR MOVE   This system consists of a single lateral on raised supports with wheels that rotates around a center point while irrigating the field. Water application rate must increase for the sprinkler units farthest away from the center of the field, since they move faster than the more centrally located sprinklers and must supply water to a larger area. Revolution rates of the unit can be from a half a day to several days. A problem with this system is that the corners of the field are not irrigated. A linear move system is similar to the center pivot, however, the entire lateral moves across the entire field rather than as a centrally pivoting lateral. Water is delivered to the moving lateral via a flexible source pipe. Both the central pivot

and the linear move systems require high capital investment but have low labor requirements.

SOLID SET/PERMANENT   A solid set system is essentially a hand-move lateral sprinkler system where enough laterals are placed in the field so that they do not have to be moved during the growing system. Water to each lateral is regulated by a series of valves. Solid set systems are removed from the field at the end of the growing season. Permanent systems consist of buried main and lateral lines, usually PVC pipe. They are not removed from the field at the end of each growing season and are most suited to perennial crops.

TRICKLE IRRIGATION   Trickle systems deliver a low volume of water under low pressure from a main source line via lateral lines. Lateral lines utilize spaghetti lines with emitters, low-rise micro-sprinklers or trickle tape (Fig. 7.4). Generally the water is applied as close to the plants as possible over a long time at low rates. One of the biggest problems with trickle systems is clogged emitters caused by particulates or precipitates from salts in the water. Nearly all trickle systems require some sort of filtering device to remove particles from the irrigation water. Media filters are used to remove organic contaminants while chemical treatment might be required to control algal growth, adjust pH or to prevent precipitation of emitter clogging salts. Routine inspection is needed to look for leaks and to correct plugged emitters and lines.

Fig. 7.4. Trickle irrigation showing lay-flat supply hose connected to trickle tape via an adjustable valve for regulating water supply.

Water quality considerations

Water quality for use in irrigation is assessed by examining its salt content. In particular, the water should be analyzed for calcium, magnesium, sodium, bicarbonate, carbonate, sulfate, chloride, and boron. In addition, water may also be tested for chemical or biological contaminants. The two factors most often considered when evaluating irrigation water are: (i) total dissolved salts (TDS); and (ii) the sodium adsorption ratio (SAR). The TDS is a measure of the concentration of soluble salts in the water (ppm), often called salinity, and is reported as electrical conductivity (EC), measured as millimhos per centimeter (mmhos/cm), deci-Siemens per meter (dS/m) or micromhos per centimeter (μmhos/cm). Since TDS may be reported in different formats by different testing labs, it is useful to convert any report to a standard value for discussion using the following equations:

1 ppm = 1 mg/l

1 mmhos/cm = 1 dS/m = 1000 μmhos/cm = 0.1S/m

*TDS (*ppm) = *EC* (mmhos/cm or dS/m × 640

SAR is the ratio of sodium to calcium and magnesium in the water. The values of TDS and SAR that would indicate water unsuitable for irrigation vary with soil, irrigation frequency, and crop. Consult a local expert for interpretation of your specific values. However, in general most water with 200–800 ppm TDS and a SAR less than 3 can be used for irrigation. Levels of TDS above 2000 ppm or SAR above 3 may severely injure sensitive species. If sodium levels are provided, most species can tolerate sodium up to 70 ppm. Above that, injury occurs. Additionally, excessive sodium harms soil structure.

Sometimes calcium can be added to irrigation water as calcium chloride, calcium carbonate, or gypsum to lower SAR. The extent of SAR reduction depends on calcium solubility in the water which depends on source and the concentration of other ions in the water. Generally, calcium chloride is more effective in lowering SAR compared with gypsum and calcium carbonate, however, it is considerably more expensive.

Carbonate and bicarbonate ions form salts with calcium and magnesium in irrigation water, precipitating out and increasing the SAR and sodium hazard of the water. Generally the formation of these precipitates can be avoided or at least reduced by lowering the pH of the water with an acid.

The boron level of irrigation water should be monitored since some crops are extremely sensitive to boron. Levels which are normal for tolerant species can cause injury in sensitive species. If boron levels are high, crop selection may need to be adjusted to avoid injury.

Excessive iron from drilled wells can clog trickle emitters and may be toxic to some species. It can be removed with a reverse osmosis filter. Toxic chemicals in irrigation water need to be removed via a media filter. Chlorine and fluorine levels in municipal water are generally not high enough to cause plant injury. Allowing tap water to sit at room temperature overnight removes nearly all of the chlorine from water used for watering houseplants.

If the water source is municipal recycled water, it may contain excessive levels of chlorine which may be toxic to plants. Chlorine toxicity generally will only occur if high levels of chlorine are sprayed directly onto the foliage. This would only occur if the water used for irrigation has come directly from treatment at a recycling plant. Free chlorine is very unstable in water and will dissipate if water is stored for a brief period before use.

Chlorinating irrigation water

Biological contaminants such as algae, fungi, and bacteria must be addressed, particularly when present in water used for trickle irrigation. These contaminants are most likely to be found in surface irrigation water sources. Filters can remove much of the contamination; however, clogging of emitters is likely over time. Irrigation water can be treated with chlorine to sanitize the water and remove the source of the clogging. Chlorination is most often accomplished by injection of chlorine into the system as chlorine gas (dangerous and expensive), or a solution of sodium hypochlorite or calcium hypochlorite. When chlorine is added to water, hypochlorous acid and hypochlorite (both collectively known as 'free chlorine') form.

Liquid household bleach is sodium hypochlorite which normally has up to 15% available chlorine. Bleach is usually added to irrigation water via a fertilizer injector. The pH of the irrigation water is often raised by adding bleach, and the available chlorine is reduced. Acid may have to be injected to lower the pH in order for the bleach to be effective.

The injection rate for sodium hypochlorite can be determined via the formula:

$$IR = \frac{(0.006 \times Q \times C)}{S}$$

Where:
IR = the injection rate
Q = the flow rate (Gpm)
C = desired chlorine concentration (ppm)
S = strength of the sodium hypochlorite source (%)

Continuous chlorine injection is needed if the water is highly contaminated. The goal is to have 1–2 ppm chlorine at the end of the irrigation system. Testing for the chlorine level at the end of the system is important since organic matter or iron and manganese can remove chlorine from the water. A good swimming-pool test kit will do the job. Periodic injection of 10–20 ppm for 2 h may be enough if the contamination is less severe. Superchlorination injections of 500–1000 ppm can be used to reclaim drip systems clogged with algae or bacteria. Expert help for superchlorination is advised since damage to plants and irrigation equipment could occur.

Calcium hypochlorite contains 65–70% available chlorine with 12.8 lb (5.4 kg) of calcium hypochlorite dissolved in 100 gallons (378 l) of water forming a 1% chlorine solution. Thus any chlorine stock solution can be made using this information. Once the concentration is known, the injection rate can be calculated from the previous formula for bleach.

Generally, the chlorinated water should remain in contact with the biological target for at least 2 h. All systems should be flushed thoroughly before fertigation or before applying a pesticide through the irrigation system.

Physiology of Water Stress

Water stress, indicating an insufficiency of water, develops as a plant's water demands exceed the water supply. It may develop rather quickly or it may develop slowly over time (often called drought stress). It may also occur diurnally, which in reality is not true water stress, but rather the inability of a plant to transpire enough water to remain turgid.

On a normal day a plant absorbs an enormous amount of radiant energy from the sun. Some of this energy is utilized in photosynthesis while most of it is not used and must be dissipated. Some is re-radiated from the plant as heat, but most of it must be removed from the plant via transpiration.

As water evaporation cools a leaf, water leaving the leaf must be replenished with water from the soil via the xylem. If the water re-entering the leaf is less than that leaving it, cells begin to loose turgor and wilt. As leaf cells loose turgor, stomata begin to close, transpiration and photosynthesis rates decline, and leaf temperature increases. Without transpiration, the temperature of the leaf can reach high enough levels to cause damage.

Turgor can be maintained by replenishing water lost from the leaf through transpiration or by adjusting the osmotic potential of leaf cells by accumulating solutes such that water is held more tightly by these cells. This process is called osmotic adjustment (OA) and is one of the first physiological responses to water stress. Cell walls can harden to maintain turgor, however, once hardened, cell growth by expansion cannot occur.

Besides cell turgor, ABA is a potent transducer of the water stress signal. As water becomes more limiting, root tissue in direct contact with drying and hardening soil produces ABA which is then transported in the xylem to the shoot. Some roots may remain moist while others dry out producing ABA and exporting it to the shoot. Thus some of the first shoot responses to water stress are induced long before the leaves sense a reduction in water supply. The stress signal from the root induces closing of stomata and an overall reduction in growth. This is a classic example of hormonal signal transduction in plants. As leaves desiccate in response to the stress, ABA is produced, amplifying the stress responses by the plant.

On the whole plant level, transpiration rate is regulated by total crop leaf area. One of the plant level responses to water stress is desiccation and abscission of older leaves, thereby reducing total leaf area and therefore the amount of water required for transpiration. A common measure often used in discussing water stress on a whole plant or crop level is the leaf area index (LAI). LAI is the total live leaf area per unit land, expressed as square meter per square meter (m^2/m^2). Transpiration increases with LAI. As a crop develops and matures, leaves abscise and the LAI as well as transpiration on a land unit basis also decreases.

Measuring plant water stress and water status

Leaf temperature is a decent quick estimate of plant water stress. The crop water stress index (CWSI) is a measure of the amount of water stress a plant canopy is under. The canopy can be a single plant or an entire field. The index is developed for irrigation scheduling using infrared temperatures of plant leaves. As transpiration decreases in response to water stress, leaf temperature relative to air temperature increases.

Leaf water potential (LWP) can be directly measured as an indication of water status. When a leaf is cut from a plant, sap under tension is pulled back into the xylem with a force equal to but opposite in sign to the LWP. The cut leaf is placed in a pressure chamber with the cut end exposed. As pressure is applied to the chamber, xylem sap is forced out of the cut petiole. When the sap appears at the petiole end, a pressure reading is taken and the LWP is estimated. LWP of live transpiring leaves is generally in the range from -0.3 MPa to -2.5 MPa.

Another piece of equipment used to estimate leaf water status is the thermocouple psychrometer. A leaf is sealed inside a small chamber with an attached thermocouple. After the sample has equilibrated in the chamber, a current is applied to the thermocouple causing it to cool. As it cools, water will eventually condense on it. More water in the leaf sample results in more water condensing on the cooling thermocouple. The current is turned off and the water evaporates which generates a signal in the thermocouple. A calibration curve is developed using various salt solutions such that the LWP of the leaf sample can be estimated.

The turgor pressure of a single cell can be measured directly with a small microcapillary tube filled with oil. The oil in the capillary moves back in proportion to the cell's turgor pressure. An estimate of the pressure on the capillary can be made by applying a balancing pressure to the capillary.

Relative water content (RWC) is often used as a measure of plant water status and is often preferred over LWP since RWC accounts for any effect OA might have on leaf water content. Two plants can have the same LWP but different RWC due to the presence of OA in one of the plants. OA involves the production of solutes by the plant which increases the osmotic potential in order to maintain higher LWP.

Osmotic potential can be measured by thermocouple psychrometry of tissue which has been frozen then thawed which releases all the solutes in the cell. Killed tissue cell sap can also be measured for osmotic potential using a micro-osmometer. Turgor can then be estimated as the difference between LWP and osmotic potential as long as both the LWP and the osmotic potential are measured using the same technique. This removes error that might be introduced by using two different techniques.

In order to estimate the amount of OA a plant undergoes during water stress, one set of plants must be carefully stressed and water stress estimated via RWC and osmotic potential measured using one of the previously described methods. The other set of plants are kept fully hydrated. OA is estimated as the difference in osmotic potential between stressed and non-stressed plants and often ranges from 0 to 1.5 MPa. Another method involves applying a predetermined amount of stress to a plant followed by overnight rehydration. Osmotic potential is then measured after rehydration and compared with a plant that was not stressed and kept fully hydrated. The OA is the difference between the osmotic potential of the two plants.

Measuring transpiration and stomatal conductance

Numerous methods have been devised for estimating transpiration rates and stomatal conductance. Gravimetric measurements simply rely on measuring how much water a plant uses in a closed system over time and expressing it as mass of water used per unit of leaf area per unit of time. Porometers can be used to estimate the transpiration of single leaves. The most common device of this type is the diffusive resistance porometer. With plants that have leaves which are difficult to reach, such as tall trees, the measurement of a pulse of heat up the tree through the xylem is measured to estimate transpiration rate.

Plant responses to water stress

Plant responses to water stress are complex and involve either adaptive changes in metabolism and overall plant structure or deleterious effects such as reduced photosynthesis and yield or leaf abscission. Coping strategies are often a mix of stress tolerance and avoidance mechanisms.

At the molecular level, there appears to be two signaling pathways in the perception and transduction of water stress, one involving ABA and the other not involving ABA. The ABA-dependent pathway involves the production of proteins in response to the water deficit which regulate genes responding to the stress. ABA may also interact with these genes without protein synthesis. The gene products can be functional or regulatory. Even though there are hundreds of drought responsive genes that have been identified, how they work to protect a plant from the deleterious effects of water stress are yet not clear.

While the immediate responses to water stress occur at the molecular level, the repercussions of such genetic regulation have profound effects on plant growth and development, and ultimately, yield. Probably the most sensitive plant response to a water deficit is reduced cell expansion. If cell expansion is reduced, growth is reduced and the water requirement is lowered. However, concomitant with reduced growth and water requirements is a reduction in yield. If the reduced growth isn't enough to maintain turgor and prevent wilting, stomata will close, reducing water loss and carbon uptake, further reducing yield.

A reduction in cell expansion also impacts meristematic tissues further reducing yield. Reduced cell expansion in meristems may lead to reduced branching and smaller reproductive organs. These effects are irreversible since once a reproductive organ has passed a certain point in its ontogeny, size is set and cannot be altered.

Flowering can be delayed or advanced depending on species. Rice flowering can be delayed by as much as 50 days by a pre-flowering water stress and this delay may be due to ABA. Water stress delays ear development but not silk development in many cultivars of corn (maize). As such, the time between silking and anthesis is greatly lengthened, with a likely reduction in yield due to inefficient pollination. A major feature of drought resistant corn is a short anthesis-to-silking interval. Pollen development is affected by drought stress with sterility often occurring under stress conditions. Another possible cause of reduced yield associated with water stress is reduced sugar production in the leaves and also translocation to developing ovaries, grain, or fruit. Root growth may or may not be enhanced by water stress. Under stress, roots of some species grow deeper into the soil.

Drought resistance

Drought resistance is often discussed as two components: (i) dehydration avoidance; and (ii) dehydration tolerance. Dehydration avoidance is the capacity of a plant to avoid dehydration at the cellular and tissue level under conditions of water stress. Dehydration tolerance is the capacity of a plant to function relatively normally under conditions of water stress. Rather than categorize plant responses as those that adopt avoidance or tolerance, we will address the plant responses that are most associated with water stress.

Roots

Deeper root systems and greater root length are both features which may allow certain species to avoid dehydration. Water-stress induced ABA maintains root elongation under drought conditions by suppressing ethylene production in the roots.

Leaves

One of the first major plant responses to water deficit is closing of stomata, which reduces the rate of water loss and carbon uptake by the leaves. Stomata close in response to ABA produced in the roots and transported to the leaves under increasing water stress. As the water stress intensifies over time, stomatal closure occurs for longer and longer periods during the day, usually starting mid-morning. With stomata closed for a longer and longer period each day, carbon fixation is reduced as well. This can ultimately lead to reduced growth and yield. In addition to stomatal closure and reduced carbon fixation due to low carbon dioxide availability, long-term carbon fixation also declines due to a slow reduction in the activity of enzymes of the Calvin cycle.

Species that are resistant to water stress show remarkable resilience in photosynthesis following rehydration after stress. In addition, photosynthesis is often less inhibited by very high temperatures (38–40°C) in dehydrated plants compared with well-watered plants, especially in resistant species.

While most of the water lost by plants is through the stomata, some transpiration does occur directly through the leaf surface. Thus, some species avoid dehydration by having very thick cuticles on their leaves. In addition, the shape of the wax crystals which are part of the cuticle can reflect solar radiation,

reducing the amount of energy that must be dissipated by transpiration. On the same lines, pubescent plants often have lower leaf temperatures and a lower water requirement than glabrous plants. This is due to several factors. The hairs create a modified boundary layer reducing water loss from leaves. In addition, the hairs reflect radiation, resulting in cooler leaves and reduced transpirational needs.

General plant stature/development

Dehydration avoidance can be accomplished by small plant size. Small plants tend to have small leaf areas and they tend to use less water. Many species that inhabit xeric landscapes are small with small leaves.

Even though water stress can lead to reproductive failure, some species avoid seasonal water stress by flowering and fruiting before the stress occurs. Other species can resist water stress during reproduction by accumulating reserves in stems and roots as soon as any stress is detected by the plant. The reserves are remobilized during reproduction.

Osmotic adjustment (OA)

A major physiological mechanism of dehydration avoidance is OA. OA results from a net increase (not just an increased concentration of) in cellular solutes, particularly potassium, sugars, and amino acids (particularly proline). OA is different in different species and develops over a long time (2 weeks). By lowering the osmotic potential of the cytoplasm, water is held more tightly by the cell, reducing or avoiding dehydration. In addition, the solutes protect proteins, enzymes, and membranes against desiccation injury. Upon rehydration after the stress, some of the solutes, particularly sugars, serve as an energy source for the recovering plant.

Oxidative damage

Some of the damage caused by water stress is from oxidative damage. Reactive oxygen species (ROS) are produced from energy not dissipated in the leaf by photosynthesis or cooling via transpiration. One of the protective measures observed in plants under water stress is a large rise in both enzymatic (superoxide dismutase, ascorbate peroxidise, and glutathione reductase) and non-enzymatic (α-tocopherol or diterpenes) antioxidants in the leaves.

Drainage – getting rid of too much water

Sometimes too much water is in the soil. Excessive water can induce as much stress to plants as too little. In this section we will examine the most widely used methods of draining excess water from agricultural land. Too much water might be the result of excessive irrigation or inadequate drainage or a combination of the two. Excessive irrigation is easily controlled with good management. Poor drainage must also be addressed (Ritzema, 1994).

Generally, if the problem is surface ponding of excess water, shallow, sloping, open drains are dug to remove the excess water. Waterlogged soil often requires a more extensive approach, often involving installing subsurface pipes to drain the water away. In either case, there are many benefits to removing excess water from production fields including: (i) a greater choice in what crops will grow; (ii) increased production; (iii) roots can grow more deeply, reaching nutrients farther down in the soil; (iv) better growth results in more efficient use of nutrients; (v) the soil structure will be enhanced over time; (vi) there are more windows of opportunity for field work; and (vii) the soil warms more quickly. Even if you have the idea that "it's not that waterlogged" or "plants are tough, they can take it", you should consider these benefits to removing excess water.

Components of a drainage system

There are three main components to any drainage system: (i) the field drainage system; (ii) the main drainage system; and (iii) the discharge outlet.

The field drainage system gathers excess water from the land using field drains and field modifications such as field sloping to promote the flow of water off the land and into the main drain. It can be surface or subsurface, and the subsurface drain can be open or a system of pipes.

The oldest and simplest form of surface field drainage is bedding. Raise beds are constructed in the field such that excess water collects in the divots between the beds and flows to a main drain. The land must be sloped to allow water movement. Beds can be formed and shaped in various configurations using manual labor, animals or mechanical

equipment (Fig. 7.5). If bedding is insufficient, land grading, and planning might be needed to achieve the desired slope for water removal. Land grading is a process in which the surface is formed to specific grades so that each field slopes towards a field drain. Compared with bedding, grading requires fewer field drains. Envision a field in which you form 20 beds, each with a field drain running to a collecting drain at the end of the field. The same field might be graded such that you only need two field drains, one on each side of the field, to carry the water away. Land planning smooths the field to remove minor imperfections in the surface topography which removes dips and depressions where water might collect.

Subsurface drains are either open systems or a system of pipes. Open drains have the advantage that they can collect excess surface water and thus also serve as surface drains. Their disadvantage is that they require constant maintenance and they use a large amount of land area and make traversing a field with equipment difficult. Pipes have the disadvantage of being expensive and they may require extensive excavation maintenance if a pipe should break or become clogged. The advantage is that once installed, maintenance is low and not much land area is removed from production.

The main drainage system receives water from the field drains and moves it to the outlet. It also collects and moves surface runoff and excess groundwater. The main drain is often a canal or series of canals. They can be open or a series of pipes.

The outlet is where the collected water is discharged into a river, lake or the sea.

Drainage requirements

When designing a drainage system, it is imperative to know the requirements for drainage of each field under consideration. The primary consideration must be determining the volume of water that must be removed from the field to enhance production. This is often not easy to do. Seasonal and year-to-year differences must be considered. The depth and extent of the water table must be evaluated. The area in the soil where water pressure is equal to atmospheric pressure is the upper level of the water table and soil pores are saturated with liquid water. Just above the water table is a region of partially liquid saturated soil, from which plants retrieve most of their water. If excessive drainage is employed, this partially saturated zone will be too low and crop growth will suffer. If drainage is insufficient, this layer will be too high and plant roots will be waterlogged. Further complicating the issue is the fact that the water table varies over time. Groundwater may be saline depending on field attributes. This must be considered in drainage plans, since salty groundwater often results from excessive salts in the soil which must be routinely leached and drained away, especially in irrigated arid climates.

A soil's hydraulic conductivity, a measure of how well a soil transmits water, is important. If a soil has low hydraulic conductivity, drainage will be more difficult.

A field's topography is important since most of the water is drained away using gravity. In addition, knowledge of any impermeable layers in the soil must be taken into account.

Detailed records and maps should be developed during construction so that future occupants of the land will know of any underground components. Notations of alterations and maintenance should also be kept.

Operation and maintenance

After installation, a drainage system must be properly operated and maintained. Unless pumps are involved, much of the operation occurs automatically. Frequent observations of the system while it

Fig. 7.5. A mechanical bed maker for pulling behind a tractor. The attachment makes beds 1 m wide and 20 cm high providing an elevated rooting environment for crops. Raised beds are often a sufficient remedy for minor drainage problems.

is operating must be made. The system should also be inspected while idle to catch and address any problems as soon as possible.

Physiological problems caused by too much water

Even though greater than 90% of a plant's makeup is water and water is absolutely essential for survival, even a small excess of water, especially in the root zone, can be lethal to plants. While there are a number of species that are quite tolerant of waterlogged soils, most crop plants do not tolerate excessive water in their root zone for any extended period. This is because water is very impermeable to gas exchange. Plant roots need oxygen to survive and function, and waterlogged soil prevents roots from receiving adequate oxygen for metabolism. It has been estimated that about 10% of farmland worldwide suffers from frequent waterlogging, reducing crop productivity by 20%.

The major consequence of waterlogging is inadequate oxygen supply to root tissue. Diffusion of oxygen through water is only about 3% that of diffusion through air, thus water-filled soil pore spaces prevent sufficient oxygen transport to root tissues. In addition, the waterlogging prevents the diffusion of ethylene and carbon dioxide away from the roots. Carbon dioxide in the soil solution can damage roots of some species (*Glycine max*) but not others (*Oryza sativa*). Waterlogging can also reduce nitrogen and iron availability in the soil and increase the levels of highly soluble manganese (Mn^{2+}) and iron (Fe^{2+}) ions which may be toxic to membranes and interfere with the activity of some enzymes. Anaerobic bacteria may convert SO_4^{2-} to H_2S, which is toxic to respiratory enzymes and non-respiratory oxidases.

Oxygen deficiency

Death of root tissue from oxygen deficiency is caused by insufficient ATP production at low oxygen levels followed by poisoning by products from anaerobic respiration. Soil water in equilibrium with air contains approximately 0.25 mol/m^3 of oxygen at 25°C, thus initially there is some oxygen in water close to the surface of waterlogged soils. Oxygen diffuses very slowly in water, thus the little bit of oxygen initially in waterlogged soil is quickly utilized.

ATP insufficiency

Aerobic roots generate sufficient ATP through aerobic respiration (38 molecules of ATP per molecule of glucose). When roots become anaerobic, ATP is generated by glycolysis (two molecules of ATP per molecule of glucose). Glycolysis also feeds pyruvic acid into fermentation producing ethanol, a potent toxin. Unless metabolic processes are limited to only essential life-supporting processes, the ATP formed through glycolysis is insufficient to maintain cell function. Most plants cannot regulate which cellular processes receive ATP and which do not, thus the lack of sufficient ATP production from glycolysis under anaerobic conditions is lethal. Under these conditions, the cytoplasm and vacuole become very acidic with negative impacts on membrane integrity. Once membrane integrity is compromised, the damage is irreversible.

The ATP produced from glycolysis relies on a supply of glucose. Quickly after anaerobic conditions commence, starch breakdown and phloem unloading cease, limiting the supply of glucose, further limiting the supply of ATP. If cells are fed glucose under anaerobic laboratory conditions, they still die, indicating that lack of a substrate for ATP production is not the sole source of death in these cells. Lack of oxygen itself for other metabolic processes contributes to cell death.

Self-poisoning

Roots under anaerobic conditions may die from self-poisoning caused by products of anaerobic metabolism. The number one toxin produced under anaerobic conditions is H^+ which causes acidification of the cytoplasm and vacuole which leads to compromised membrane integrity.

Acetaldehyde is another potential toxin. Acetaldahyde is produced from pyruvic acid by pyruvate decarboxylase. Acetaldehyde is then converted to ethanol by alcohol dehydrogenase. The rate of ethanol production from acetaldehyde usually exceeds the conversion of pyruvate to acetaldehyde. When tissue is returned to aerobic conditions, this regulation is sometimes lost and a toxic level of acetaldehyde may develop.

Nitric oxide, a free radical gas, formed by nitrate reductase under anaerobic conditions may be toxic enough to kill root tips. Some scientists suggest that death of root tips by nitric oxide might be a survival mechanism under anaerobic conditions.

Root tips may die, but the rest of the root can survive if the anaerobiosis is not too long. Once the anaerobiosis is gone, dormant buds on surviving roots can begin to grow, replacing damaged tips.

Surviving anaerobiosis

The level of oxygen in the soil and soil water slowly declines as a soil becomes waterlogged subjecting roots to a period of hypoxia which may induce biochemical or anatomical changes which support survival of anaerobic conditions.

BIOCHEMICAL ADAPTATION If plants are exposed to slight soil oxygen stress for 6 h before aerobic conditions, survival is increased from 8 h to 72 h in some species. The mechanism for sensing the slight stress is unknown. The slight stress induces the production of anaerobic proteins, enzymes involved in: (i) energy metabolism; (ii) pH regulation; (iii) aerenchyma formation; (iv) ROS scavenger production for when roots return to aerobic conditions; (v) signalling; and (vi) yet others which have unidentified functions. If the synthesis of these proteins is inhibited, the acclimation reaction is not observed. Concomitant with production of these enzymes is a coordinated reduction in the demand for oxygen, substrates, and ATP.

ANATOMICAL ADAPTATION — AERENCHYMA FORMATION Species that grow well in wet soil often have very large intercellular gas-filled spaces all the way from the shoot to the root tip. This tissue is called aerenchyma tissue. The air spaces are created by differential division and expansion of adjacent cells or by death of certain cells. Enough oxygen can diffuse through aerenchyma tissue to supply the roots up to 30 cm from the shoot with sufficient oxygen for metabolism.

Most species do not possess aerenchyma tissue. There are a few species (e.g. *Z. mays*) that can produce aerenchyma in roots during the early stages of reduced oxygen supply during waterlogging. The aerenchyma formed is a result of cell death in the root cortex that is stimulated by increased ethylene concentration. The increased ethylene concentration is due to increased production and reduced ethylene catabolism. Death of specific cells begins in about 6 h of elevated ethylene and is complete within 2 or 3 days. Cell death is an ordered sequence of events which is not well understood.

SHOOT TOLERANCE OF LOW SOIL OXYGEN LEVELS Shoots and roots are intimately linked, so it is no wonder that low oxygen levels in the roots eventually affects physiology of the shoots. Since nitrogen uptake and metabolism in the root is curtailed with waterlogging, young leaves begin to utilize nitrogen remobilized from older leaves. The older leaves senesce prematurely. Waterlogged plants also tend to wilt (not epinasty) under bright light due to a reduced capacity for water uptake by roots in a low oxygen environment.

Rapid signaling from the roots to the shoots during waterlogging decreases stomatal opening and leaf expansion. In some species like tomato (*Lycopersicon esculentum*) a marked epinasty of leaves occurs. Epinasty is the downward 'wilting' appearance of leaves under excess water conditions caused by increased cell division on the adaxial (upper) side of the leaf petiole. This reduces the angle of light incidence on the leaf blade, reducing water loss.

How are leaves signaled to become epinastic? Roots under anaerobic conditions export the ethylene precursor 1-aminocyclopropane-1 carboxylic acid (ACC) to the shoots via the xylem. ACC is exported to the shoots due to increased ACC synthesis and reduced oxidation of ACC to ethylene in the roots as a result of low oxygen in the roots. ACC builds up in the root tissue and enters the transpiration stream. Finally, leaf petioles have an enhanced ability to oxidize ACC within 6 h of waterlogging, caused by enhanced ACC oxidase synthesis in the petiole.

In waterlogged conditions, shoot bases of some species undergo changes that may enhance survival of roots under anaerobic conditions. These changes include development of aerenchyma tissue in lower shoots or hypertrophic lenticel development in water-covered shoot bases. Lenticels are groups of specialized cells on stem, root, or fruit tissues, much like stomata on leaves, which enhance gas exchange. Hypertrophic lenticels are enlarged lenticels. Another response often involves the production of replacement roots near the surface of the soil. Replacement roots near the soil surface may occur through the stimulation of growth in pre-formed root initials or the initiation and subsequent growth of root initials at the stem base. Both processes are induced by ethylene. Another root growth alteration to help survival in anaerobic conditions is the upward growth of lateral roots towards the soil surface.

Using Water to Regulate Temperature

Evaporating water uses energy. This energy is removed as heat from the object water is evaporating from. This fact is utilized in several areas of horticulture including: (i) postharvest produce cooling; (ii) cooling of greenhouses; (iii) cooling of growing crops in the field during high temperatures; and (iv) reducing heat unit accumulation in orchard trees to delay bloom.

Cooling with evaporation requires an understanding of wet bulb and dry bulb temperatures and their impact on evaporation. The dry bulb temperature is the temperature we all know as the air temperature. It is readily available from weather reports or from a thermometer. The wet bulb temperature is the lowest temperature the air could be cooled to via evaporation. When your skin is wet and the wind is blowing, the temperature you perceive cooling is the wet bulb temperature. The wet bulb temperature is a measure of the amount of water in the air. Wet bulb temperatures are available from the local weather station or measured directly with an aspirated or sling psychrometer.

A psychrometer consists of two thermometers. One is called the dry bulb. The other is called the wet bulb and has a cotton wick surrounding its bulb and the wick is immersed in water. Air is forced over both bulbs either by a fan (aspirated psychrometer) or by twirling the unit (sling psychrometer) to create a stream of air. The air passing over the wet bulb wick evaporates water until the wet bulb temperature is reached. The other bulb supplies the dry bulb temperature.

If a psychrometer is not available, the wet bulb temperature can be calculated from the RH, which is easily obtained from a weather station. (RH can be measured with an electronic humidity meter, but these often need to be recalibrated quite often. A psychrometer is the better choice.)

Knowing the wet bulb temperature provides an estimate of the maximum cooling potential of evaporation.

Cooling produce

Evaporative cooling can be used to cool harvested produce. It can be used for the initial removal of field heat from the commodity and it can be used to cool produce during storage. The cooling process involves misting the produce, usually in the presence of air with 65% RH or less. The maximum temperature reduction possible through evaporative cooling is 6–8°C, and the amount of cooling actually achieved can be quite variable. A general rule of thumb is that you can cool to about 1 or 2°C above the wet bulb temperature of the air.

To minimize the amount of field heat that must be removed, it is best to harvest early in the day when field heat is minimal. Keep the produce as cool as possible until it can be brought to storage. Produce can be pre-cooled prior to storage by misting it and allowing the water to evaporate. Even though this may only reduce the produce temperature by a few degrees, it is an inexpensive method for reducing the cooling load of the permanent storage cooler. It certainly is less expensive than other pre-cooling methods such as forced air, hydrocooling, or vacuum cooling.

Cooling greenhouses

Most greenhouses reach excessive temperatures during the summer growing season and are unfit for crop production unless cooled. Evaporative cooling is the most widely used method of greenhouse cooling (Bucklin *et al.*, 2011). Air conditioning can be used, but installation and operation costs are prohibitive.

To obtain a measure of potential cooling with evaporation, obtain the wet bulb temperature in the early afternoon. This is when maximum cooling will be required. With a well-managed and maintained system, the greenhouse temperature can be cooled to within 1 or 2°C of the wet bulb temperature.

Evaporative cooling of greenhouses is accomplished by evaporating water into an airstream. This is most often accomplished using what is called a fan and pad system. High pressure fogging systems can also be used to evaporatively cool a greenhouse. They provide more uniform temperatures and humidity in the house, but are substantially more expensive.

The fan and pad system consists of an exhaust fan located at one end of the greenhouse which draws outside air through a vent at the other end of the greenhouse. As the air enters the greenhouse through the vent it passes through a porous pad, usually made of cellulose, through which water is trickled with a circulating pump. It is important to have a tightly sealed greenhouse so that air enters only through the pad to maximize evaporation. Water evaporates and cools the air

entering the greenhouse. Each gallon of water evaporating removes 8100 BTUs (British thermal units) of heat from the air entering the greenhouse. Air is coolest immediately after passing through the pad and entering the greenhouse and warms slightly as it approaches the fan. The temperature gradient should be as small as possible. Air may warm by as much as 1°C every 6 m it travels. Additionally, the cooled air tends to travel in an angle up and away from the plants it was intended to cool. In a cross-greenhouse flow configuration, this is usually not a problem, as gutters connecting roof sections of large greenhouses provide baffles to deflect cool air downwards. In smaller greenhouses, the distance from side to side is short, thus the air divergence is not of great concern. In lengthwise-flow configurations, baffles should be created every 10 m and extend from the roof of the greenhouse down to just above crop level.

If the efficiency of the cooling system is known, the temperature of the air exiting the cooling pad can be estimated as follows:

$$T_{cool} = T_{out} - (\text{Percentage efficiency})(T_{out} - T_{wb})$$

Where:
T_{cool} = the temperature of cooled air
T_{out} = the temperature of outside air
T_{wb} = the wet bulb temperature of outside air

A well-designed system can have an efficiency of up to 85%. To illustrate how effective pad cooling systems can be, a system with 85% efficiency can take outside air at 32.2°C and 50% RH down to 24.7°C. That's a 7.5°C decrease in temperature.

Regulating bloom in fruit crops

Many deciduous species require exposure to moderately low temperatures (0–5°C) for a species-specific duration (chill units) in order to complete endodormancy. After fulfillment of this chilling requirement, buds will grow and develop upon exposure to warmer temperatures. Evaporational cooling with water can be used to increase chill units accumulated or reduce heat unit accumulation. Increasing chill units promotes bloom by terminating endodormancy, while reducing heat unit accumulation delays bloom to avoid frost or freeze injury (Alfaro *et al.*, 1974; Anderson *et al.*, 1975; Bauer *et al.*, 1976; Buchanan *et al.*, 1977).

Terminating rest in fruit crops

Deciduous fruit crops are often grown in climates marginal for chilling. Instead of switching to other crops, attempts have been made to artificially provide chilling. One method is to reduce solar energy absorption by buds with reflective materials such as white latex paint or kaolinite clay. This approach has met with very limited success (Glenn *et al.*, 2002). Another method uses evaporational cooling with water to reduce bud temperature, thereby increasing chill unit accumulation to break endodormancy (Gilreath and Buchanan, 1979; Hewett and Young, 1980). Overhead irrigation or misting can cool dormant buds by 4–6°C during chilling accumulation. Bud break following overhead irrigation to enhance chilling is often accelerated by a week or so compared with non-irrigated controls. This may be a response to increased chilling or may be a response to leaching of water-soluble plant growth regulating substances from the buds.

Drawbacks to this method are: (i) the expense associated with irrigation; and (ii) the potential for increasing plant susceptibility to frost and freeze injury and disease.

Delaying bloom in fruit crops

Evaporational cooling has been considered as a means for reducing heat unit accumulation early in the spring thereby delaying bloom in some fruit crops (Chesness *et al.*, 1979). Temperatures of buds can be reduced to nearly the wet bulb temperature and bloom has been delayed by as much as 10–18 days depending on species.

As in irrigating for enhanced chill unit accumulation, potential problems with irrigating to delay bloom include: (i) the expense of irrigating; (ii) orchard waterlogging; and (iii) increased susceptibility of sprinkled buds to freeze damage and disease.

Crop cooling

Some fruit, particularly apples (*Malus domestica*) and brambles (*Rubus* spp.), may be subject to sunburn. This occurs when the fruit surface temperature is too high for an extended period. Even 1 day of excessive fruit temperatures can cause damage. Sunburn appears as a discoloration of the fruit skin. In brambles, individually burnt drupelets appear white. One method for reducing

fruit surface temperature is by overhead irrigation (Parchomchuk and Meheriuk, 1996).

Fruit can be cooled by convection, which is cooling of the air by evaporation of water into the air (Unrath and Sneed, 1980). The cooled air then cools the fruit. Fogging systems cool by convection, but they must be run continuously to be effective. Fruit can also be cooled directly by applying cold water to the trees in fruit. The cold water absorbs heat from the leaves and the fruit, thereby cooling them. Overhead irrigation provides this type of cooling. It does, however, require a tremendous amount of water which may lead to other problems (waterlogging, water wastage, nutrients leaching from the soil). The most effective method of cooling fruit is using evaporative cooling. This method of cooling removes heat from tissues by evaporating water off their surfaces.

An effective cooling system for fruit in the field should strive for a maximum amount of evaporative cooling, since it is most effective. The effectiveness of the system depends on: (i) RH; (ii) wind speed; (iii) water application rate; (iv) temperature; and (v) grower ability. Growers must be able to ensure that the system can be run for the duration of the potential sunburning season. Even 1 day missed could effectively wipe out the entire season's efforts for reducing sunburn.

Fruit injury can occur if the fruit temperature is at or above 30°C. Fruit temperature should be monitored just below the skin on the sunny side of the fruit. Fruit in full sun can reach temperatures as high as 50°C even when the air temperature is much lower. Careful monitoring of fruit temperature is critical. The system should be turned on when the fruit temperature reaches 2°C below the critical temperature. Thus in general, the system should be turned on when the fruit temperature is 28°C. The system should be turned off when the fruit temperature falls below 28°C.

The idea of fruit cooling is to keep the fruit from reaching the critical temperature, not cooling the fruit down once it reaches that temperature. The irrigation system must be able to supply enough water to keep the fruit below the critical temperature. The on-off cycle timing for the system should be such that maximum evaporative cooling occurs with a minimum amount of water application. Application of water in pulses to keep the fruit surface wet so that water is always evaporating from the fruit surface. Excessive water application does not enhance cooling and is wasteful of water and energy.

Red fruit color in apple (*M. domestica*) can be improved with fruit cooling in some growing regions. Fruit color is enhanced in 70–80% full sun with day/night temperatures both less than 27/10°C, respectively. Generally, cooling for this purpose begins 4 weeks before harvest. Cooling should commence 30 min before sunset and last until 60 min after sunset. In addition to improved color quality, crop cooling increases soluble solids, fruit firmness, and average fruit weight. It has also been shown to reduce corking and bitter pit in apple.

Crop cooling may leave chemical residues on the fruit after evaporation. Most often, the residue of concern is calcium carbonate. Analysis of the water used for cooling will provide clues as to whether or not precipitates left after cooling might be a problem. Some of the following indicate a potential problem: (i) a pH of 7.8; (ii) EC above 3 mmhos/cm; (iii) calcium or magnesium concentrations of 50 mg/l; and (iv) carbonate or bicarbonate levels of 100 mg/l.

Water requirements for crop cooling must be considered when calculating total crop water requirements. Water used for crop cooling does not supply appreciable water as irrigation. Thus, water used in cooling must be subtracted from the total water available, thereby reducing the water available for irrigation. Since most growers have a finite water supply, drip irrigation is a good way to save irrigation water, making it available for cooling.

Frost protection using water

Water in plant cells is not pure. It contains dissolved sugars, salts, and proteins. Thus the freezing point of plant cells is usually one to several degrees below 0°C. Most plant tissues are not injured at 0°C, thus keeping a plant at a temperature very close to 0°C can prevent freezing injury.

Overhead irrigation is used to prevent frost injury to fruit crops in many fruit growing regions of the world. Several important properties of water make this possible. One is that approximately 1 calorie of heat must be removed per gram of water for each 1°C reduction in temperature. In other words, water gives of a little energy as it cools. The second property which is much more significant in frost protection strategies is that 80 calories of heat are released for each gram of water freezing when water freezes at 0°C.

A third factor which is often overlooked in discussions on frost protection with irrigation is the

fact that when both solid and liquid water co-mingle, the temperature of the mixture will neither go above nor below 0°C until the phase change is complete. That is, the temperature stays at 0°C until all the water freezes or all the ice melts. The basic idea of frost protection with water is to maintain a thin film of water on the plant, even if the film is over a layer of ice. As long as the film of liquid water is present, the temperature of the tissue being protected will not fall below 0°C. Contrary to popular belief, the freezing water does not warm the plant or the air around it.

The plant must be able to support the weight of ice formed during protection. With low-growing crops such as strawberry (*Fragaria* × *ananassa*) this is generally not a problem. With tree fruit such as peach (*Prunus persica*) or apple (*M. domestica*), this can be a significant concern.

The protocol for frost protection with irrigation must be followed precisely for success. Irrigation must be turned on early enough in the evening to compensate for the evaporational cooling of the air that is likely to occur when the system is first turned on. Adequate volume of water application must be maintained during the frost event to ensure a thin layer of liquid water on the crop as sprinkler heads revolve during application. If too little water is applied, the phase change to ice may be complete before the next quantity of liquid water is applied, and the temperature of the plant may drop below freezing causing injury. Finally, a liquid layer must be maintained until all of the ice has melted following sunrise. If the irrigation is turned off too soon, the temperature of plant tissue may fall below freezing due to evaporational cooling or cooling caused by ice sublimation.

Undertree misting or irrigation can be used for frost protection but it does not afford the same level of protection as overcrop irrigation and it works via a different mechanism. Undertree systems operate by applying a film of water near the surface of the soil via short misting or irrigating risers. The water freezes releasing heat energy which is then transferred to the crop above. In addition, the layer of ice that forms on the soil surface reduces radiational cooling, keeping the orchard warmer than non-irrigated orchards. Tissues are not encased in ice as with overhead systems, and the system does not operate continuously. Undertree systems provide only about 1–3°C protection and are effective only if the wet bulb temperature is near 0°C. Colder dew points lead to excessive evaporational cooling which could totally negate any protection afforded by the freezing water.

In general, overtree irrigation may provide up to 6.7°C protection while undertree systems may provide up to 2.8°C protection. The advantage of undertree systems is that water application can be pulsed rather than applied continuously, thereby reducing water use. In addition, undertree systems can also take advantage of smaller nozzles which also reduces water use. While smaller nozzles can be used with overhead systems, their use is tricky as they may not provide sufficient volume and coverage.

Mass Flow and Movement of Assimilates in Plants

The movement of assimilates in the phloem in plants is investigated in this section on water since the movement of phloem solutes depends on water and is intimately connected to water in the xylem. Plants move assimilates (primarily sugars) through the phloem using water and metabolic energy.

Mass flow – simplified

The generally accepted hypothesis for how assimilates move within a plant is called the Mass Flow Hypothesis (also called Pressure Flow Hypothesis). Glucose, manufactured in the leaf during photosynthesis, is converted to sucrose (a dissacharide composed of a molecule of glucose attached to a molecule of fructose). Sucrose is then actively loaded into sieve tubes of the phloem (living cells). Movement of sucrose into the sieve cells of the sieve tube causes the water potential of these cells to become more negative. This more negative water potential creates a gradient which draws water from neighboring xylem cells into the sieve cells. This in turn creates a pressure. The phloem sap will begin to move along the sieve tube due to the pressure gradient caused by the water movement into the sieve cells where the sugar was initially loaded.

Once the sap reaches a sink (such as a developing fruit, dividing cells of a meristem, or storage cells in the root) sucrose molecules are actively unloaded from the sieve cells of the sieve tube to mesophyll cells in the sink tissue. As this happens, the osmotic potential of the sieve cells becomes less negative and water begins to leave the sieve cells of the sieve tube. The sucrose is used for metabolism, used to

synthesize cellulose or converted into starch for storage. Starch is 'nice' for storing energy in a carbohydrate because it has no effect on the osmotic properties of the cell in which it is located. The water that leaves the sieve tube eventually returns to the xylem for the long trip back to the leaf.

This is mass flow, simplified. In order for this incredible phenomenon to occur, some rather fascinating things must happen at the cellular and tissue level. Let's look at the phloem a little more closely.

The phloem

Phloem consists of: (i) parenchyma cells for storage; (ii) fibers for support; (iii) sieve cells (also called sieve elements) for transport; and (iv) companion cells for metabolic help. Sieve cells, which are relatively long and slender compared with other cells, are placed end to end forming sieve tubes, an extensive conduit in which to transport phloem sap. At the ends of each sieve cell are large-diameter, membrane-lined pores called sieve pores, collectively called a sieve plate. As sieve cells develop, much of their protoplasmic contents degenerate leaving a functioning plasmalemma with protoplasm containing only a few plastids, mitochondria, and some smooth endoplasmic reticulum near the cell wall. Thus a functioning sieve tube is a long series of connected sieve cells with functioning protoplasm with few organelles. In other words, it is full of phloem sap and that's about all.

If the sieve cell is pretty much an empty cell, how does it survive? That's where the companion cells come in. Each sieve cell has one or more companion cells intricately connected to it via plasmodesmata, and together they form the sieve cell–companion cell complex. Companion cells have many ribosomes, mitochondria, and rough endoplasmic reticulum along with a prominent nucleus. The companion cell performs the metabolism sieve cells need to survive. Without companion cells, sieve cells would die.

What happens if one of these long tubes is damaged? Phloem sieve cells have a very effective mechanism for plugging sieve plates if necessary. Sieve cells are under high turgor pressure. Any rapid loss of pressure in a sieve cell causes a specific phloem protein (P-protein) to quickly plug up the pores in the sieve plate. Callose, a carbohydrate, is also produced in response to wounding or high temperature stress to plug the pores. Once plugged, that sieve tube no longer functions in long-distance transport of assimilates. It can function in transport up to the point of plugging.

Phloem sap

Phloem sap is mostly water. A general description of the contents of phloem sap based on a number of species would include: (i) it is 10–12% dry matter; (ii) it has a pH of 8.0–8.5; and (iii) it has considerable solutes in it, mostly non-reducing sugars and also amides, amino acids, organic acids, potassium, and trace amounts of auxins, gibberellins, cytokinins, and ABA. These solutes generate an osmotic pressure of 1.2–1.8 MPa.

Carbohydrates transported in the phloem are non-reducing sugars where the reactive aldehyde or ketone group of the molecule has been reduced to an alcohol, usually mannitol or sorbitol, or combined with a similar group from another sugar to form an oligosaccharide. Sucrose is the most widely transported sugar. There are some exceptions. Sorbitol is the principal transport sugar in members of the family *Rosaceae* and stachyose is the predominant transported sugar in members of the *Cucurbitaceae*.

Phloem transport occurs in the range of 2.8–11 g/m^2 phloem/s. Phloem sap has been estimated to move at speeds of up to 56×10^{-5} m/s or 200 cm/h.

Mass flow – in depth

Translocation in the phloem is caused by pressure gradients, derived from differences in osmotic pressure due to active loading and unloading of solutes from sieve cells. Solutes are loaded into sieve cells at the source end (leaf) of the phloem. This causes the osmotic pressure of the sieve cell to become more negative, water enters the cell and increases the pressure within. The increased pressure forces the contents in the phloem to flow towards the area of lower pressure existing at the sink end of the phloem (fruit, meristem, storage roots). At the sink, the solutes are actively unloaded from the sieve cell, causing the osmotic pressure to be less negative, and water leaves the cell, thereby reducing the pressure.

The main question surrounding the Mass Flow Hypothesis is whether or not sufficient pressure exists within the phloem to make it work. Direct measurement of pressure in the phloem is difficult. However, indirect estimates support the hypothesis in this regard. Another important question is

whether or not the pressure gradient is steep enough from source to sink to generate the phloem flow observed. Estimates of the gradients between source–phloem–sink are sufficient to account for the flow observed.

The phloem has a tremendous capacity for transport. As previously noted, phloem transport normally occurs in the range of 2.8–11 g/m^2 phloem/s. A phloem transport rate of 305 g/m^2 sieve-tube area/s was observed in castor bean when the pressure at the sink end was removed by cutting the fruit pedicel and allowing flow to occur unobstructed. This observation indicates that crop productivity does not seem to be regulated by phloem transport but rather by loading and unloading of the phloem. Phloem has the capacity to transport a tremendous amount of assimilate.

Since movement of assimilate from source to sink seems to be primarily regulated by loading at the source and unloading at the sink, let's look at the two processes.

Phloem loading

Phloem loading occurs primarily in the leaves. To be exact, phloem loading is the process of photoassimilate transport from photosynthesizing mesophyll cells in the leaf to sieve cells in the phloem. Most loading into sieve cells occurs in the minor veins of a leaf while the transport occurs through major veins. Minor vein ends consist of a single xylem element, a few parenchyma cells and one or two sieve cells symplasmically connected to one to four companion cells.

Photoassimilates can travel from mesophyll cells to sieve cells via plasmodesmata or by exiting the mesophyll cell through the plasma membrane, travelling through the cell wall and then into a sieve element traversing its plasma membrane. The former is called symplasmic phloem loading and the latter is called apoplasmic phloem

loading (Fig. 7.6). Which path sugar molecules take is still a source of debate. A broad generalization is that more primitive species utilize symplasmic phloem loading while more highly evolved species use apoplasmic phloem loading. Many herbaceous species and most crop plants belong to this latter group. Some species utilize both pathways.

With either apoplasmic or symplasmic loading, the mechanism for doing so must account for selective loading of solutes into sieve cells and the resulting elevated solute concentrations within the sieve cell–companion cell complex.

Symplasmic loading

Most plants that load assimilates symplasmically translocate between 20 and 80% of the sugars in a raffinose-related compound such as raffinose, stachyose, or verbascose. The general hypothesis is that sucrose diffuses from mesophyll or bundle sheath cells into companion cells via plasmodesmata. Once in companion cells, sucrose is enzymatically converted into oligosaccharides (raffinose and stachyose) which maintain a diffusion gradient for sucrose. Raffinose and stachyose are larger molecules than sucrose and are prevented from diffusing back into mesophyll or bundle sheath cells by size-excluding plasmodesmata. The raffinose and stachyose diffuse into sieve cells.

Apoplasmic loading

The apoplasmic loading model accomplishes selective concentration of solutes in sieve cells via an energy-dependent membrane transport pump. Genes have been identified which are selectively expressed in leaf phloem which encode this sucrose pump. Unfortunately not much is known about sucrose efflux out of mesophyll cells.
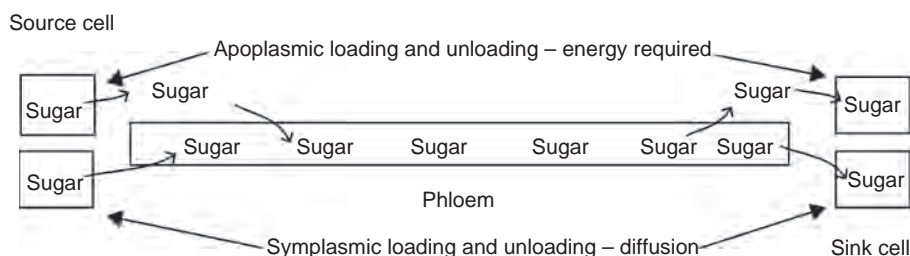
Fig. 7.6. The mass flow model of phloem transport: phloem loading and unloading.

Regulation of flow

When the source is limiting photoassimilate transport due to less-than-maximum synthesis at the leaf, changes in sink demand have no effect on the rate of transport. In other words, even if sink demand is high, during fruit growth for example, the flow in the phloem is controlled by the synthesis of sugar in the leaf. On the other hand, if the source is not limiting, any change in sink demand greatly changes export from the leaves. If demand is high in the sink, phloem flow will be high if there is sufficient assimilate being produced in the source. Sink regulation of transport from the source by sinks is likely via effects on the sucrose-loading membrane pumps in the leaf, most probably controlled by pressure changes in the phloem. The response to pressure would occur within minutes. Gibberellin applied to leaves leads to a rapid increase in photoassimilate loading into the phloem.

Phloem unloading

The final step in the phloem transport chain is unloading products of photosynthesis into the sink, or phloem unloading. Once at the sink, the transported photosynthates have one of three fates: (i) cellular catabolism in respiration; (ii) biosynthesis of components needed for growth and maintenance; and (iii) conversion into storage products that regulate transport among competing sinks. Phloem unloading is actually composed of two distinct components: (i) unloading from the sieve cell; and (ii) transport to the sink cell. While phloem loading occurs within a very specific framework, from mesophyll cells to sieve cells in a leaf, phloem unloading occurs over a much broader framework.

Unloading can occur in root or shoot apices, various cells of the stem or root, vegetative storage organs, or reproductive organs. Unloading also occurs in different cell types such as differentiating sieve cells, sieve cells lacking companion cells, or sieve cells with active companion cells. Cells into which the phloem is unloading may be dividing or expanding and the metabolism of these cells may vary from respiration to synthesis of components of growth, maintenance, or storage. In order to accommodate these various configurations for phloem unloading, a wide range of mechanisms of unloading exists.

Pathways of unloading

Unloading phloem solutes take one of three cellular pathways: (i) apoplasmic; (ii) symplasmic; or (iii) symplasmic–apoplasmic–symplasmic. Photoassimilates can be directly unloaded across the plasma membrane of sieve cells into the apoplasm of sink cells. This is apoplasmic unloading and it occurs especially in radial unloading to storage parenchyma cells in roots and stems. If the assimilate moves directly from cell to cell with no entrance into the apoplast, travelling through plasmodesmata, symplasmic unloading occurs. This is typical in apical meristems of shoots and roots as well as vegetative storage organs such as potato tubers. In some situations, the assimilate must leave the symplast, temporarily entering the apoplast, before re-entering the symplast as it is unloaded into sink tissue. Developing seeds demonstrate this type of unloading. There is an apoplasmic space separating symplasts of maternal and filial tissue in seeds which prevents totally symplasmic transport. Another example is the transport of assimilates from root tissue to mycorrhizas or from stem tissue to mistletoe.

Once unloaded, transport through the sink tissue is primarily symplasmic. Since symplasmic transport does not involve membrane transport, resistance to flow is much less in symplasmic transfer compared with apoplasmic transport.

In some situations, the mode of transport switches, especially in developing sinks such as fruit. The tomato is a good example. Early in fruit development phloem unloading is symplasmic. Sugars are converted into starch in sink cells, maintaining a pressure gradient for further phloem unloading. Later during fruit expansion, transport switches to an apoplasmic route. This is necessary because during expansion, sugars are not converted into starch. As such, osmotic pressure is generated in sink cells. In order to avoid shutting down phloem transport due to building pressure in sink cells, the phloem is 'separated' from the sink via the apoplasm.

Mechanism of unloading

Since the concentration of sugars in sieve cells is high, a concentration gradient exists that facilitates leakage of sugars into the apoplasm. Some of this sucrose is reloaded back into the sieve cell by membrane-bound pumps, thus the total amount of

sucrose unloaded via diffusion is determined by the concentration gradient inside and outside of the sieve cell as well as the activity of the membrane pumps.

Symplasmic transport occurs via cytoplasmic streaming and movement through plasmodesmata. The limiting phase of the process appears to be movement through plasmodesmata.

In the seed system where there is an apoplasmic barrier between two symplasmic steps of phloem unloading, the efflux of assimilate from the first symplasmic phase into the apoplasmic phase occurs via a sucrose–proton antiport membrane pump (sucrose out, proton in). Sucrose uptake from the apoplasmic phase into the second symplasmic phase occurs via a sucrose–proton symport membrane pump (sucrose in, proton in).

Fate of unloaded assimilates

Once unloaded, assimilates may be used for respiration, biosynthesis of components needed for growth and maintenance, or conversion into storage products.

What happens to assimilates depends on the sink cell function. No matter what the specific function of the sink cell, part of the imported assimilate is used for respiration in cell maintenance. In growing cells, some of the imported assimilate is used for synthesis of cell materials. In general, approximately 40% of assimilates are used in respiration and 55% is used for growth materials. In mature cells, much of the imported assimilate is stored (about 80%) as insoluble starch in vacuoles or amyloplasts or sugar compartmentalized in the vacuole. Stored sugars are usually sucrose, hexoses, or fructans (short-chain polymers of fructose). Sucrose and hexoses are particularly important in fruit and vegetable quality, while fructans are important in pasture forage quality or remobilized for storage in the grain. The storage carbohydrate may change during development. For example, young fruit of tomato store starch while maturing fruit store hexoses, and convert stored starch to hexoses. The rest is needed for maintenance respiration. Storage may be short (hours or perhaps days) or long term (months to perhaps years).

Author Query

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