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Managing Drought Stress in California Agricultural Systems

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Abstract

California is currently facing a historic drought, and this has led many farmers in the state to severely cut back on irrigation. Optimal use of water for irrigation requires a comprehensive understanding of how plants respond physiologically to water stress (Chapter 1). By monitoring water requirements in crops and managing irrigation to meet those requirements, growers can significantly reduce water use (Chapter 2). This can be done through improving application efficiency of irrigation technology as well as increasing the water use efficiency of the crops themselves. Deficit irrigation practices can be used to manipulate the physiology of water use in plants and increase crop tolerance to drought stress. Imposing minor stress on plants induces chemical signaling within the plant that decreases stomatal aperture, increases root to shoot ratio and manipulates root architecture to optimize water gain and reduce loss. Though these practices have reduced yield compared to conventional irrigation, these reductions are minimal in most cases and can be considered better than severely reduced yields due to poor irrigation planning. Ultimately, deficit irrigation practices increase the yield obtained per unit of water applied. Additional benefits have also been reported with the use of deficit irrigation, such as improved yield quality and reduced shoot vigor.

Monitoring irrigation is an essential first step to optimal irrigation management, and it is an intrinsic part of integrated pest management. Drought stress affects the dynamics of certain plant pathogens and arthropod pests in both

positive and negative ways, and this is important to consider when utilizing deficit irrigation practices. Often, avoiding plant stress is crucial, but this is not simply achieved by watering to avoid drought stress. It is important to create the best environment for healthy plant growth, and this may often mean reducing irrigation when necessary to improve a crops tolerance to drought stress and/or pest pressure (Chapter 3).

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Preface

For the past two years, I have been interning in the western United States, mostly working in the area of plant diagnostics for diseases and pests and agricultural research. From May to September 2014, I worked for Oregon State University in their plant pathology diagnostic lab in the Columbian Basin on the arid side of the Cascade Mountains. We saw mostly cases involving potato pathogens, including fungal, bacterial, and viral diseases, but we also encountered samples of various vegetables and some horticultural specimens. I also took part in testing potato psyllids for infection with the Zebra Chip bacterium (Cand. *Liberibacter solanacearum*).

From May to July of 2015, I worked in the Central Valley near Fresno with California Agricultural Research, a company that mainly dealt with GLP (Good Laboratory Practices) Regulatory trials involving Pesticide Residue where my main duties included monitoring pest and disease problems and advising on how to manage them. Starting in September 2015, I took a position at Pacific Ag Research Group in San Luis Obispo, California. I was responsible for starting up and maintaining their newly built pathogen lab, where I maintain a collection of mostly fungal pathogens and help design, prepare and implement disease and other trials.

Having lived in Nebraska for the duration of my doctoral degree work, I had learned about the current drought in California and how severe it had become. However, the summers of 2014 and 2015 allowed me to witness firsthand the consequences of this historic drought on agriculture in one of the worst hit areas of California. Beginning in 2014, when I was driving from southern California up to eastern Oregon, I began to notice an amazing number of dead orchards and fallow fields, especially toward the center of the state, alongside signs that read, “No Water, No Jobs” and “Congress Made Drought.” These signs were in reference to the sever rationing of water not only in response to the drought, but also the allocation of water to be released in the delta to protect endangered fish species. The drought had compounded the issue of water rationing and many farmers in the Central Valley were forced to rely on wells that were quickly drying up or forced to scale back production.

In the Columbian Basin of Oregon, the issue was quite different. The Columbia River that flows from the Northern Rockies is very large by the time it reaches the Oregon-Washington border. As a result, there is little restriction on water access in the Columbia Basin agricultural area, even though it is considered very arid. Growers tended to over irrigate in this valley, using mostly sprinkler and pivot irrigation, and I saw many cases of disease problems that arose from poor irrigation both here and in California.

Previously I had read some very interesting research on irrigation strategies that were reported to improve both water use efficiency and crop quality by actually maintaining a degree of drought stress on crops, and this is what inspired me to write my doctoral paper. Since irrigation is a fundamental part of growing crops in semi arid regions, I wanted to explore possible strategies for coping with water scarcity and exactly what is the best way to irrigate. Much of the research that I read pointed to the idea that water should not just be applied to increase yield, for this eventually leads to diminishing returns, but that optimal water use may actually require irrigating less than conventionally thought.

Chapter 1: Physiology of Drought Stress

Introduction

California's average annual precipitation ranges from 5 inches or less in the Imperial Valley and desert southeast to up to 200 inches in the Northwest of the state (Figure 1.1) (USGS, 2005). In the prime agricultural regions of the state, the average is between zero and twenty five inches per year. Further, the region is dominated by a Mediterranean climate in which most of the precipitation falls between November and February and is stored as either snowpack or in groundwater basins. Consequently, most crop production is irrigated and depends on stored water, especially during the summer months when precipitation amounts to less than one inch.

Despite the arid nature of the agricultural regions of California, they are among the most important production areas in the United States and, for some commodities, the world. In 2013, California produced the most cash receipts ($46.4 billion) of all states in the US (USDA, 2015). California produces 80% of the world's almonds, 40% of the world's Pistachios, and 90% of grapes grown in the US (USDA, 2015).

In 2011, California began one of the worst droughts in modern history when winter precipitation fell below average. By 2014, California reached the third driest year on record in recent history (Figure 1.2), preceded only by 1924 (during the Los Angeles-Owens valley water wars) and 1977 (Miller, 2014). By June 2015, water cutbacks for cities were mandated of up to 25% reduction of potable urban water use (Kostyrko, 2015). Prior to this mandatory reduction, farmers in the Central Valley were already denied their full, contracted allocation of surface water from the Sacramento River Delta according to a 2007 ruling (NATURAL RESOURCES DEFENSE COUNCIL, et al. v. DIRK KEMPTHORNE et al., 2007). The ruling was in response the the NRDC lawsuit against the EPA to reduce pumping from the southern end of the Sacramento San Joaquin Delta in an effort to reduce salinization and protect the endangered Delta Smelt and reduced water allocation by around 50% (Fresno County Farm Bureau, 2007).

The winter of 2015 and 2016 has been characterized by a strong El Niño weather pattern with increased precipitation, but it is unclear whether there will be sufficient precipitation to declare an end to the current drought or when and how severe the next drought will be. With a growing population, demand for fresh fruits and vegetables, increasing pressure to protect endangered species and increasingly restricted access to fresh water, growers in California have to produce crops with less water or face going out of business. Novel irrigation technology and techniques are allowing growers to reduce water use up to 50% while maintaining yields, improving crop quality in certain cases and even reducing the severity of some pests and pathogens. This document summarizes the effects that drought stress has on crops and how technology and crop management practices are changing to meet these challenges.

Water is essential for plant growth and reproduction as a medium for biochemical reactions and cellular integrity. The chemical characteristics of water give it properties that best support life. Water molecules have a dipolar structure with two free pairs of electrons and the slightly positive charge from two hydrogen atoms. This polarity makes it highly self-cohesive and a good solvent. The hydrogen bonds formed between water molecules also impart a high specific heat and latent heat of vaporization, both of which enable plants to regulate internal temperature when properly hydrated. A high specific heat means water must absorb a large quantity of energy to increase in temperature, and conversely, must lose the same to decrease in temperature ($4.19 \text{ J g}^{-1} \text{°C}^{-1}$ @ 20° C). A high latent heat of vaporization (2454 J g^{-1}) allows water to remove energy from leaf tissue as it evaporates from within the leaf because of the energy needed to completely break hydrogen bonds. This evaporative cooling buffers against high ambient temperatures and internal leaf temperature increases resulting from the capture and processing of light in photosynthetic reactions in leaf cells.

Water transport in plants

Water transport from roots to shoots is driven by evaporation from leaf mesophyll cells and diffusion through stomata. As water evaporates from curved surfaces in cell wall matrices, a negative tension is created that pulls water from xylem vessels. Through actions of cohesion and adhesion, primarily due to hydrogen bonding, xylem vessels act like a wick that draws water from moist soil. However, water transport and evaporative cooling require a great deal of water and plants tend to lose around 90% of the water they take up from the soil through transpiration (Davenport, Hagan, & Uriu, 1977).

There are two points of resistance to water diffusion out of the leaf: stomatal resistance and boundary layer resistance. A small amount of water can escape through the cuticle, but this is negligible compared to water diffusion through stomata. Gas exchange only takes place through stomata, causing water loss and carbon dioxide fixation to be tightly linked. When stomata are open, roughly 50 to 400 molecules of water are lost for every molecule of carbon dioxide that is fixed, depending on the efficiency of photosynthesis in the plant (Taiz & Zeiger, 2010). In regulating water loss through stomata aperture, carbon sequestration suffers due to reduced diffusion of carbon dioxide into the leaf.

Plants regulate water loss and carbon dioxide intake by regulating stomata pore aperture. In plants not experiencing drought stress, stomata open in response to light on a diurnal pattern and aperture widens or narrows in response to CO_2 concentrations and ambient water vapor (Taiz & Zeiger, 2010; Mansfield & Meidner, 1966). However, drought stress has a strong influence on stomata closure to reduce water loss, as will be discussed in more detail.

Some plants are able to compensate for reduced CO_2 diffusion through variations in leaf anatomy and carbon metabolism. As apposed to C3 plants which have the site of RUBISCO activity (the main enzyme involved in carbon sequestration) in close proximity to internal leaf cavities where CO_2 diffuses to, C4 plants physically separate the site where CO_2 is sourced in the leaf and where carbon is fixed in bundle sheath cells. New carbon atoms are chemically fixed to phosphoenol pyruvate to eventually form the four-carbon molecule malate. Carbon dioxide is then released into the cytoplasm of bundle sheath cells effectively increasing CO_2 at the site of carbon sequestration. This allows C4 plants to reduce stomatal aperture and prevent water loss while being able to cope with resulting lowered CO_2 concentrations in leaf air space (Taiz & Zeiger, 2010). Most crops grown in large quantities in California are C3 plants and very few C4 crops, that include grasses such as corn wheat and barley, are grown in the state.

Factors that influence water loss and gain

Water loss is influenced by vapor pressure deficit, temperature and wind. Vapor pressure deficit is the difference between internal leaf saturation vapor pressure and ambient air vapor pressure or a measure of how dry the air is compared to internal leaf humidity. Thus, it depends on relative humidity and temperature. Relative humidity is a measure of the water vapor quantity in the air $rh = \frac{e_{air}}{e_{s_{air}}}$ x 100%, where e_{air} is the saturated vapor pressure of air. Drier air has a much lower water vapor pressure than internal leaf spaces. Under such conditions, plants loose more water if stomata remain open. Drought conditions in semi-arid regions are defined by weather systems dominated by dry air, with a shorter or more infrequent wet season, increasing the length of time during the year where vapor pressure deficit can be elevated.

Temperature has a two-fold impact on evapotranspiration. Besides affecting the relative humidity of ambient air, temperature contributes to the heat energy input into the liquid phase of water within the leaf, as well as the saturation vapor pressure of water vapor within internal leaf spaces. Combined, these effects act to increase transpiration demand.

Wind exacerbates water loss due to its effect on the boundary layer that forms around leaves. The boundary layer is a layer of still air at the surface of the leaf that contributes to the total resistance of water vapor diffusion out of the leaf. Increased wind speeds disturb this layer of still air, effectively reducing its thickness and the resistance to water vapor diffusion out of the leaf. Daudet et al. (1999) found the following relationship between wind speed (U in m-s^{-1}) and boundary layer conductance g_b^H (mm-s^{-1}) as: $g_b^H = 10U + 7.1$. This equation demonstrates a ten fold increase in conductance (the inverse of resistance) with each additional m per second increase in wind velocity.

Water supply to the plant is determined by available soil water content. This depends on characteristics of the soil, such as texture, organic matter content, and soil structure. Sandy soils tend to have less water holding capacity and a smaller range of volumetric water content available to plants. Loam soils (soils containing a mixture of soil particle sizes) tend to have greater water holding capacity and available soil water content (ASW) than sandy soils, with silt loam usually containing the largest range of ASW. Available soil water content is reduced in clay soils, even though they tend to have the highest water holding capacities, due to a greater ratio of micropores to macropores (Bronick & Lal, 2005). Water drains more easily from macropores and is held tightly in micropores by cohesive and adhesive forces. Water availability to plants is dependent on a proper range between the two pore classes, when the difference between field capacity (all but the largest of pores are filled such that no excess water drains) and wilting point (soil water tension is stronger than a plant's ability to withdraw it) is the greatest (Bronick & Lal, 2005). Soil organic matter can improve the structure of soils so pore size range can be maintained through microbial activity, producing microaggregates containing micropores and surrounded by macropores (see review by Bronick & Lal, 2005 for more information). Also, organic matter itself has a large water holding capacity (Hudson B. D., 1994)

Effect of water stress on cell growth

The greatest impact of water stress is seen on cell growth (Hsiao, Acevedo, Fereres, & Henderson, 1976). Cell growth and division in plants is dependent on irreversible cell expansion due to turgor pressure (ψ_p) and cell wall extensibility (m) (Hsiao & Xu, 2000). This relationship, first proposed by J. A. Lockhart in 1965, has been found to have a threshold potential (Y) below which no cell expansion can take place and above which the relationship is linear (Matthews, Volkenburgh, & Boyer, 1984). The slope of cell wall extensibility depends on cell wall extension response (Green, et al., 1971; Nonami & Boyer 1990).

$$\begin{aligned}&\text{for } \psi_p > Y\\ &G = m(\psi_p - Y)\\ &\text{for } \psi_p \le Y\\ &G = 0\end{aligned} \tag{1}$$

The rigidity of a plant cell wall is controlled by inherent properties of the cell wall and new cell wall production. Plant cell walls are a combination of cellulosic fibers that have a high tensile modulus (10^{11} N m^{-2} (Cosgrove, 2000)) surrounded by a hemicellulose matrix that includes glycans that connect the cellulose fibers. The tautness of these connecting glycans is controlled by proteins called expansins that are believed to loosen the polysaccharide bonds between cellulose fibers through the “turgor-driven polymer creep” model first proposed by McQueen-Mason and Cosgrove (1994).

McQueen-Mason, Durachko, & Cosgrove (1992) discovered these proteins in a groundbreaking experiment where they added plant proteins to denatured cell walls under pH of 4.5 in an extensionometer and found that cell wall expansion resumed. Expansin activity is stimulated by a decrease in extracellular pH induced by auxin activated proton pumps (Cosgrove, 2000). At an intercellular pH of 7 no cell wall relaxation is observed. In response to increased auxin production in the growing region, proton pumps can decrease external pH to around 4.5, increasing expansin activity. Generally, the cell wall becomes more rigid in drought hardened plant cells. The threshold potential goes up, requiring more turgor for growth, and cell wall extensibility goes down, becoming more rigid and increasing growth effective turgor ($\psi_p - Y$) (Matthews, Volkenburgh, & Boyer, 1984). This results in greater sensitivity of shoot growth to additional drought stress, a mechanism that prevents excessive vigor and water loss.

Water uptake (g in s^{-1}) depends on the growth-induced water potential gradient ($\psi_o - \psi_w$, where ψ_o is the external water potential and ψ_w is the internal water potential) across the cell wall/membrane and the volumetric hydraulic conductance (L), which is controlled by aquaporin permeability.

$$g = L\,(\psi_o - \psi_w) \qquad (2)$$

When combined, equations 1 and 2 give a growth rate of:

$$G = (mL/(m + L))(\psi_o - \psi_s - Y) \qquad (3)$$

where $\psi_s = \psi_w - \psi_p$ and is the internal osmotic potential of the cell (Nonami & Boyer, 1990). This equation demonstrates that growth rate is directly related to the difference between osmotic potential gradient across the cell membrane ($\psi_o - \psi_s$)

and the threshold potential (Y), indicating that threshold potential and osmotic potential are important to growth rate. It also indicates that the product of cell wall extensibility and hydraulic conductance, and their sum, form a ratio and the relationship between growth rate and either of these parameters is more complicated than osmotic potential (ψ_s) and threshold potential.

By measuring these parameters in soybean (*Glycine max*) seedlings transplanted from moist soil to water deficient vermiculite, Nonami & Boyer (1990) found that, while the growth induced water potential gradient ($\psi_o - \psi_w$) increased after subjection to growth media with a lower water potential, the hydraulic conductance (L), cell wall extensibility (m) and the growth effective turgor pressure (ψ_p –Y) were slow to recover, reaching 50% or less of their original values after three days. This indicates that actively growing plant cells are conditioned to reduce cell growth in response to drought events.

Root sensing mechanisms to drying soil

Roots sense changes in water potential of drying soil through hyperosmolality sensing proteins, and also possibly through changes in root cell water status, mechanical changes in root cell volume or both. The response is a signal cascade, mainly regulated by the stress hormone abscisic acid that affects both roots and shoots. Recently, Robbins & Dinneny (2015) wrote a detailed review of the research on hydrotropism, or the active growth of roots towards areas of higher water potential or water content, and water stress sensing and response summarized here. Yuan et al. (2014) demonstrated that the *A. thaliana* gene OSCA1 (Reduced Hyperosmolality-Induced Calcium Ion Increase 1) is involved in cytosolic

Ca^{2+} increases characteristic of early drought stress response (Knight et al. 1997). Mutants lacking the gene did not show increased root growth or exhibit stomatal closure in response to sorbitol treatments to reduce water potential. Other genes implicated have been Arabidopsis Histidine Kinase1 (AHK1) (Urao, et al., 1999), Mechanosensitive Channel Of Small Conductance-Like (MSL) (Kloda & Martinac, 2002) and Feronia (FER) (Shih , et al., 2014). AHK1 proteins are osmolality-sensing proteins in high concentration on stomata of *A. thaliana*. However, mutants lacking this gene have shown no change in osmotic adjustment due to drought stress (Kumar, Jane, & Verslues, 2013). MSL proteins one and two are similar to bacterial osmolarity-sensing proteins and are found on organelles, regulating their internal water status in relation to cytosolic water potential. FER proteins are receptor-like kinases involved in mechanoreception, especially in hypoosmotic stress, and may be involved in hydrotropism.

Role of abscisic acid in root to shoot signaling of drying soil conditions

In response to drought stress, roots produce abscisic acid (ABA), a plant stress hormone that has three crucial roles in drought response: stomata closure in leaves to regulate water loss, inhibit shoot growth, and recovered root growth. ABA is transported through the xylem to aerial organs (Davies, et al., 2000). These responses lead to greater water uptake and decreased water loss by increasing root to shoot ratio and preventing excessive water loss through open stomata. In some plants, such as tomato (Holbrook, Shashidhar, James, & Munns, 2002) and sunflower (Fambrini et al. 1995), evidence suggests that stomata respond to ABA produced in leaves as well.

Xylem sap has also been demonstrated to become more alkaline in response to drought stress and has been proposed to act synergistically with ABA to influence stomata closure (Schachtman and Goodger 2008). Abscisic acid is a weak acid (pKa=4.7) and is absorbed passively by mesophyll cells in non-ionic form. Kaiser and Hartung (1981) found an exponential decrease in ABA absorption in mesophyll cells with increasing apoplastic pH. Alkaline pH is believed to lead to an increase in apoplastic ABA concentrations and ABA receptor binding to plasma membrane ABA G protein coupled receptor (GCR2 in *Arabidopsis thaliana* (Liu, et al., 2007)) in guard cells. However, Schachtan and Goodger (2008) point out that stomatal response to increased apoplastic pH varies between species and some plants such as soybeans close stomata under drought conditions long before their xylem sap pH increases.

Abscisic acid binding to guard cell receptors stimulates cytosolic calcium ion levels via reactive oxygen species formation, primarily nitric oxide and hydrogen peroxide. The internal increase in calcium ion concentration affects a number of signals that lead to stomatal closure. Primarily the increase in Ca^{2+} causes an efflux of anions, mostly Cl^-, through slow- (S-gated) (Linder & Raschke, 1992) and rapid-gated (R-gated) ion channels (Hedrich, Busch, & Raschke, 1990), and membrane depolarization triggering a potassium ion efflux by opening outward potassium ion channels (Schroeder, Raschke, & Neher, 1987). Conversely, elevated Ca^{2+} concentrations in the cytosol inhibit inward potassium cation channels and outward proton pumps (Lemtiri-Chlieh & MacRobbie, 1994; Schroeder & Hagiwara, 1989). The latter can lead to a significant pH increase of the apoplast immediately surrounding the guard cells that also inhibits inward potassium cation channels.

Calcium influx also induces the release of calcium, chlorine and potassium ions from the vacuole (Schroeder, et al., 2001). ABA stimulates nitric oxygen, cADPR and IP3 production that stimulate vacuolar calcium efflux as well. The net effect is an increase in osmotic potential of stomatal guard cells and loss of turgor pressure, and this deformation relaxes guard cells, reducing stomatal aperture (Schroeder, Allen, Hugouvieux, Kwak, & Waner, 2001).

Effect of ABA on root and shoot growth

In response to ABA and other drought stress signals, root cells rapidly adjust osmotically in order to reduce internal water potential lower than external water potential and modify cell wall chemistry in the meristem, allowing them to maintain growth under low water potentials (Hsiao & Xu, 2000; Westgate & Boyer, 1985). Abscisic acid has the opposite effect in shoot meristems in that endogenous ABA treatment inhibits shoot growth, possibly due to its effect on stomatal aperture and consequently photosynthesis (Blum, 2011) and the fact that cell walls in shoot meristems become more rigid and apoplastic pH tends to be high. Further, the osmotic adjustment that shoots experience to maintain turgor is much slower than that in root tips (Hsiao & Xu, 2000).

Research is still being conducted on the exact nature of signaling pathways for osmotic adjustment in root meristems. While evidence has suggested ABA regulates the increase of some solutes involved in osmotic adjustment of root cells, some researchers have reported ABA independent signals for solute accumulation. For instance, ABA signals have been shown to directly regulate accumulation of the amino acid proline (Yamaguchi & Sharp, 2010) and possibly indirect K+ ion transport (Osakabe, et al., 2013). Proline accumulation is considered a major contributor to osmotic adjustment during drought stress, accounting for up to 45% of solute contributions to decreased osmotic potential in maize primary roots (Voetberg & Sharp, 1991). Osakabe et al. (2013) demonstrated that a series of potassium pumps in the K+ uptake transporter (KUP) family and guard cell outward rectifying K+ channel (GORK; a potassium efflux transporter) are indirectly regulated by ABA signaling and expressed in root growing tips during drought stress in *A. thaliana*. However, Verslues & Bray (2006) found that osmotic adjustment was independent of ABA signaling in *A. thaliana*. They found that proline accumulation, which may contribute to osmotic potential and has roles in reactive oxygen species scavenging and other protective roles, increases in response to ABA signaling.

More clearly understood is the effect of ABA on cell wall extensibility in roots. Abscisic acid promotes auxin accumulation in root tips, likely via isoflavanoid and flavonoid production, leading to acidification of the cell wall necessary for expansin activity (Yamaguchi & Sharp, 2010). Xu et al. (2013) found that, in addition to increased ABA accumulation in roots, auxin transport to root tips also increases. Through experiments with *Arabidopsis* and rice, primary root tips exposed to 5% polyethylene glycol (PEG) to reduce water potential to -0.48 MPa, or exogenous ABA at 0.1µm, they found a significant increase in root elongation and proton efflux in the growing region between the two treatments and the control, but no difference between treatments. *Aba*3-1, which is responsible for conversion of ABA-aldehyde to ABA, the final step of abscisic acid (ABA) biosynthesis (TAIR, The Arabidopsis

Information Resource, 2006), mutants subjected to PEG showed no difference in root elongation rate or proton-ATPase activity, but exogenous ABA treatment allowed for the recovery of both.

In another experiment, Xu et al. (2013) found that 24 hour exposure to either PEG or ABA treatments caused increased primary root elongation rate, plasma membrane H^+-ATPase activity, proton extrusion, and root hair density. When plants exposed to fluoridine, an ABA synthesis inhibitor, all parameters were strongly inhibited. Concurrently, auxin levels in the root tip were significantly elevated in the PEG and exogenous ABA treatments. Inhibitors of auxin influx reduced all root growth parameters in the control plants and impeded root growth parameters under low osmotic potential (with PEG) or when exposed to exogenous ABA.

ABA also affects a number of other hormones involved with root growth inhibition, such as ethylene (Sharp, 2002), and plays an important role in reactive oxygen species (ROS) protection by regulating the expression of several ROS response genes. These include metal chelating proteins like metallothioneins and ferritins, proteinase inhibitors, proline accumulation and flavonoid production pathways in the growing region of roots (Yamaguchi & Sharp, 2010). Metallothioneins chelate heavy metal ions, such as iron and copper, and ferritins chelate free iron, metals which can react with hydrogen peroxide to form hydroxyl radicals. Proteinase inhibitors are thought to be important to prevent the degradation of oxidized proteins, allowing for recovery from oxidative stress that may inhibit root growth. Proline and isoflavanoids act as antioxidants as well;

however, proline and isoflavanoids have significant roles in the maintenance of root growth under low soil water potential.

Effect of drying soils on root architecture: role of cytokinins and auxin in hydrotropism

In addition to inducing recovered and maintained root growth under moderate drought, drying soils also affect the architecture of root zones in many plants. Exposure to periodic drought stress causes roots to grow deeper into the soil profile and access soil horizons that retain plant available water longer. In grain crops such as sorghum and wheat, drying topsoils have been shown to induce "compensatory growth" in deeper roots resulting in prolonged exposure to available water (Blum, 2011).

Roots sense gradients in water potential and exhibit a phenomenon known as hydrotropism in which root tips bend in the direction of greatest water potential. Hydrotropism is still not completely understood on the cellular level; however, studies with *Arabadopsis* mutants have shown several key components. Abscisic acid stimulates amyloplast shrinkage in columella cells so that gravitropism can be overridden (Cassab, Eapen, & Campos, 2013). The NHR1 and AHR1 genes, both directly regulated by ABA, are involved in reduced amyloplast size, because mutants lacking both retain normal sized amyloplasts during hydrotropic stimulation and ABA treatment (Cassab, Eapen, & Campos, 2013). Amyloplasts are degraded in water stressed roots as well as in response to hydrotropic stimulation (Cassab, Eapen, & Campos, 2013). ABA and cytokinin are currently thought to modulate auxin-controlled gravitropism.

Lateral roots also form in response to water potential stimulus (Robbins II & Dinneny, 2015). In an experiment by Bao, et al. (2014), *A. thaliana* roots developed more lateral branches on the side exposed to greater water potential. They showed that auxin signals build locally in response to contact with water and induce lateral bud formation. While auxin promotes lateral root branching in the pericycle, cytokinins inhibit root branching during water stress and promote primary root growth by inhibiting auxin gradients that form lateral roots (Blum, 2011, p. 39; Laplaze, et al., 2007). Cytokinins act on genes like the *A. thaliana* gene MIZ1 produced in root tips and hydrathodes (Cassab, Eapen, & Campos, 2013). MIZ1 encodes unkown protein with a domain found in proteins in several plant species. Overexpression of MIZ1 reduced lateral root growth and mutant MIZ1 roots showed “increased levels of auxin” and insensitivity to cytokinin signals. Babé et al. (2012) found that this suppression takes place in root segments of barley and maize growing during water deprivation as short as 4-8 hours in a hydroponic system. Frequent watering of topsoil layers induces greater root development in shallow layers since hydrotropism outweighs gravitropism, an important concept to remember when dealing with water management of established crops.

Damage due to severe drought stress

Under more severe drought stress, cavitation, or the formation of air bubbles in xylem vessel water columns, can break the flow of water to shoots and reduce the ability to transport water to outer shoots in plant canopies. In many cases plants adapt to this damage by blocking off cavitated vessel elements and producing alternativie xylem tissue. However, shoot dieback has been associated with hydraulic conductance failure due to cavitation under severe drought circumstances in *Ceanothus crassifolius*, a chaparral plant considered to be drought tolerant (Davis, Ewers, Sperry, Portwood, Crocker, & Adams, 2002).

Nutrient uptake as well as fruit and shoot development are also hindered under drought stress, affecting yield and long-term health of plants, especially perennials. Water shortage in the soil reduces the dissolution and mobility of mineral nutrients, limiting their absorption by plants and their translocation to growing shoots. Nitrogen, phosphorous and potassium are most affected by drought stress.

Water shortage effects the mineralization and availability of nitrogen in the soil because microbial activity in the soil and mobility of nitrogen is reduced under water deficits (Bloem, Deruiter, Koopman, Lebbink, & Brussaard, 1992). Hu and Schmidhalter (2005) found that differences in in yield response to nitrogen fertilization in winter wheat are only noticeable under irrigated conditions in sandy soil, indicating the wheat was only receptive to extra nitrogen when well irrigated.

Phosphorous deficiency occurs early in drought stressed plants (Turner, 1985) and is translocated acutely less to the shoots of maize seedlings under even mild stress (water potential between -0.5 and -1.0 MPa) of the growth media in response to treatment with PEG (Rasnick, 1970). However, supplementation of phosphorus can reduce drought stress, possibly due to its positive effects on stomatal conductance, photosynthesis, and cell wall membrane integrity (Hu & Schmidhalter, 2005). Hu & Schmidhalter (2005) also point out the soils in semi- and arid regions tend to be more alkaline and bind phosphorus more readily.

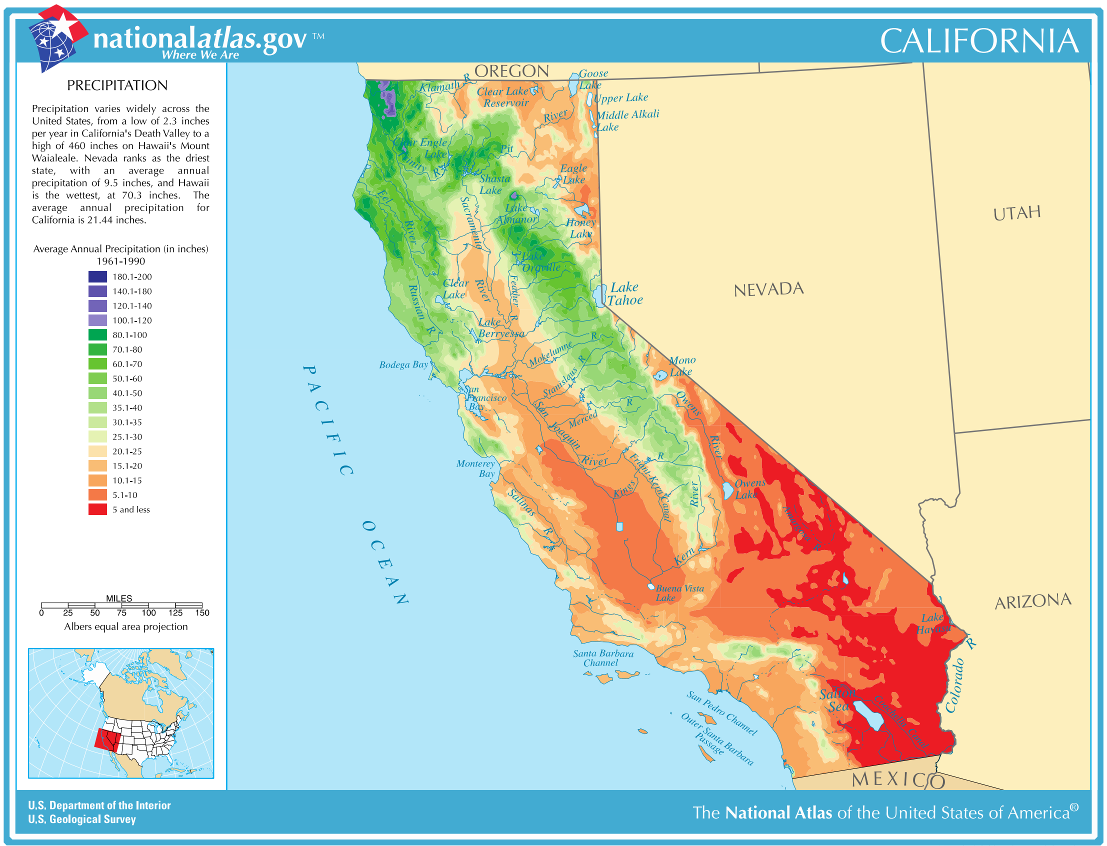
Potassium ions become less mobile in water deficient soils. Potassium aids in "stomatal regulation, osmoregulation, energy status, charge balance, protein synthesis, and homeostasis (Beringer & Trolldenier, 1978; Marschner, 1995; Hu & Schmidhalter, 2005)." Potassium is also instrumental in maintaining turgor pressure (Mengel and Arneke, 1982), and reducing transpiration under drought conditions (Andersen et al., 1992; Hu & Schmidhalter, 2005). Potassium is also a significant ion in solute accumulation under drought stress conditions contributing to about 78% of all solutes in wheat (Morgan, 1992) and 25% in rapeseed under drought stress (Ma, Turner, Levy, & Cowling, 2004). Calcium is also limiting under drought stress, but not as severely as the prior three. Regardless, calcium ions play an important role in drought stress signaling (Hu & Schmidhalter, 2005), as well as an integral atom in cell wall formation.

Carbon shortages associated with reduced transpiration and closed stomata can affect fruit development and cause shoot dieback. For example, in citrus trees carbon shortages cause fruitlets to abscise prematurely because sugar transport acts as an inhibitor to abscission whereas the ABA/ethylene pathway induces abscission (Iglesias, et al., 2007). During water stress, citrus tends not to abscise leaves or developing fruit but will suddenly do so upon rehydration, leading to a reduced photosynthetic potential in the short term, and possibly tree death if the abscission is severe enough. This is thought to be caused by reduced xylem flow from stressed roots to aerial tissues. The main signal for abscission is 1-aminocy clopropane-1-carboxylic acid (ACC), the precursor to ethylene, produced in drought stressed roots. Reduced xylem flow prevents ACC from being transported to leaves and fruitlets. Concurrently, ABA increases in leaves and developing fruit and gibberellic acid decreases in developing fruit, inhibiting any further shoot growth. Rehydration allows for increased mobility of ACC to mature leaves and fruits as well as fruitlets where it can be metabolized to ethylene and promote abscission. In young leaves, auxin production counteracts the effects of ethylene, allowing them to be retained (Iglesias, et al., 2007).

Depending on the species or variety, environmental conditions, and crop load, drought stricken citrus trees may experience a greater flowering rate upon recovery, especially in tropical regions or subtropical regions with mild winters. Second to cold weather, drought stress induces greater inflorescence. Though more flowers may seem to lead to an improvement in yield potential, late season flowering and branches with a greater flower to leaf ratio have a lower fruit set. A higher leaf to flower ratio on a flowering shoot increases the chance of fruit set and yield on that shoot (Iglesias, et al., 2007). This is most likely due to photoassimilates that are produced in the leaves of flowering shoots (Syvertsen & Lloyd, 1994). It may be that drought reduces fruit set through this response to previous water shortages.

In almond trees, severe water stress before hull split can cause reduced hull split, necessary for almond harvesting, and reduced kernel size (Goldhamer, Viveros, & Salinas, 2006). Trees may experience leaf yellowing and abscission as well as shoot dieback (Fulton, et al., 2016), reducing future photosynthetic capacity. Minor stress can improve grape quality by concentrating sugars and other soluble solids. However, severe stress in grapes can lead to premature leaf and tendril abscission (when experienced during mid season), reduced bud formation, yield, berry size, and maturation (especially when experienced early in the season) and dieback (Ojeda, Deloire, & Carbonneau, 2001).

Pistachio trees experiencing 50% or less of crop evapotranspiration have a reduced hull split and yield, as well as a greater number of empty shells. Premature leaf yellowing and abscission have also been observed, and yield reductions can be carried into the next year, even if normal irrigation resumes (Goldhamer, et al., 1985). Vegetable crops experience wilting, yield loss, nutrient deficiencies, and reduced quality of fruit or harvestable parts. One example of this is blossom end rot in tomato, which occurs when developing fruits do not get enough calcium required for proper cell wall formation. Subsequently, tomato fruits experience rotting symptoms at the floral bud scar. It is important to manage irrigation optimally in semi arid to arid irrigated agriculture to reduce water usage while mitigating water stress damage and yield reduction and for a maximum profit margin.



Precipitation varies widely across the United States, from a low of 2.3 inches per year in California's Death Valley to a high of 460 inches on Hawaii's Mount Waialeale. Nevada ranks as the driest state, with an average annual precipitation of 9.5 inches, and Hawaii is the wettest, at 70.3 inches. The average annual precipitation for California is 21.44 inches.

pageprecip_ca3.pdf INTERIOR-GEOLOGICAL SURVEY, RESTON, VIRGINIA-2005

Figure 1.1. Annual average precipitation in inches for California between 1961 and 1990 (USGS, 2014)

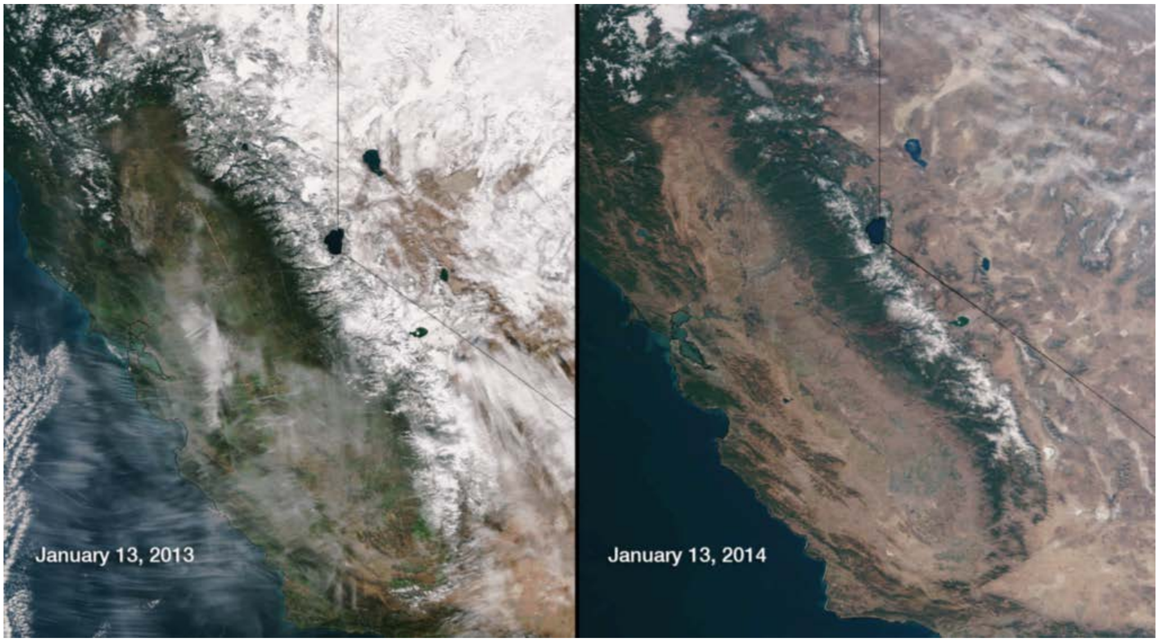


Figure 1.2. Satellite images of the snow pack on January 13, 2013 (left) and 2014 (right) (NOOA, 2014)

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Chapter 2: Increasing Irrigation Efficiency: From Flood To Trickle.

Irrigated agriculture is one of the oldest human endeavors, dating back to as far as 6000 BC when canals were built along the Nile in Egypt or the Tigris and Euphrates in Mesopotamia (modern day Iraq) (Irrigation Association, 2014). Over time, irrigation and water transportation technology has advanced to: 1) deliver water to fields, as well as city centers, further from the source, 2) allow for greater efficiency and 3) store water over longer periods of time to allow for us during drier periods of the year. As a result, by the year 1800, irrigated land reached 19.76 million acres worldwide and 600 million acres by the year 2014 (Irrigation Association, 2014).

As of 2010, 62 million acres of land was irrigated in the US and 10 million acres in California (16% or 25.8 million acre-feet) compared to Nebraska's 6.3 million acre-feet or 8.73 million acres (14%) of land in the same year. (Maupin et al., 2014), making California the largest withdrawer of water for irrigation of all states in 2010. In response to the current drought, farmers in California are looking toward increasingly more efficient irrigation methods. This chapter discusses a few of these strategies and how irrigation has evolved over time as well as other strategies to increase irrigation efficiency.

Methods of Irrigation

Until the invention of the sprinkler in the late 19th century (Lessler, 1871), irrigation was mainly delivered to fields through flooding. Furrow irrigation is an irrigation strategy in which crops planted in raised ridges are flooded and water allowed to infiltrate the soil. Water is either pumped into the field or fed through siphon tubes that use gravity and suction to deliver water from canals into the field with no mechanical action.

Furrow irrigation is an easy and relatively cheap way to irrigate in terms of logistics, cost, and equipment. However, the water use efficiency, defined as the amount of yield or biomass produced per amount of water supplied, can be as low as 30% (Hillel, 1997) to no more than 60% (Stein, 2011). The USGS estimates that only half of the water used in flood irrigation supports crop growth, while the rest is most likely lost to transpiration, evapotranspiration, and runoff (USGS, 2015), especially in dry, hot weather or heavy rain events. Leaching of mobile nutrients, such as nitrates, can also be an issue, particularly if there are large amounts of runoff from the field. However, some leaching is necessary to reduce salt deposits in agricultural fields (Hillel, 1997). Prolonged flooding also causes stress similar to that of drought and a number of soil diseases thrive when the soil is poorly drained.

In spite of its inefficiency, furrow irrigation is still widely used in the country and in California. In 2010, furrow irrigation was the second most utilized strategy in the US, with 26.2 million acres or 42% of irrigated land in the US (Maupin M. , Kenny, Hutson, Lovelace, Barber, & Linsey, 2014) and 43% of irrigated agricultural land in California (Tindula, Orang, & Snyder, 2013).

Efforts to increase furrow irrigation efficiency have been studied because of the convenience and low cost of flood irrigation. Surge flow furrow irrigation can improve application efficiency by 15% (Amosson, New, Bretz, & Marek, 2001) by surging water flow into furrows incrementally using a surge valve. This method allows for the stream front to traverse the length of furrows faster and reduces deep percolation closer to the valve (Goldharner, Alerni, & Phene, 1987). Cutoff irrigation is a practice in which water moisture is monitored at different points of the field from the headgate to the end of the field, and fields are flooded only until the water front reaches the bottom of the field (ODA, Oregon Department of Agriculture). This application method is a tradeoff between thoroughly irrigating the entire field and preventing water loss through deep percolation and surface evaporation. Application efficiency of this method depends on the soil type and infiltration rate, but can improve application efficiency by reducing losses to deep infiltration and overflow (Raine & Bakker, 1996).

Sprinkler and pivot irrigation is another common practice in field crops. However, in California it only accounted for 15% of irrigated agriculture in 2010 (Tindula, Orang, & Snyder, 2013). Sprinkler irrigation is the most widely used irrigation strategy in the US, constituting 31.6million acres (50.6 percent) of US irrigated land in 2010 (Maupin M. , Kenny, Hutson, Lovelace, Barber, & Linsey, 2014). Water propelled sprinklers commonly used in agriculture were first invented in 1871 for use in lawns by Joseph Lessler (Lessler, 1871) and improved upon by Orton Englehart, founder of Rainbird, in 1935 to automatically turn by using water pressure pushing against an undulating, spring propelled arm for force (Englehart, 1935).

The original center pivot (Figure 2.1), invented in 1948 by Frank Zybach, consisted of sprinklers mounted on a boom two feet above the ground and supported by metal skids (Mader, 2010; Gaines, 2015). The center was connected to a water source fed by a pump and supported by a tower from which the pipe rotated. The outer end was moved mechanically by two wheels attached to another tower (Mader, 2010; Gaines, 2015). Since then, many modifications have been made to pivot irrigation to make it more applicable and efficient. The boom, now known as a span, was raised to above 6 feet to accommodate tall crops such as corn, and a truss was placed under the span to support the weight of the water. Motorized wheel towers replaced the metal skids to support the center of the pivot pipe. Pivot sprinklers are either placed above the transport pipe or suspended from rubber hoses that can be raised or lowered from the boom to water above or below the canopy.

Traditionally, sprinklers were operated at 20 to 30 psi and located above the canopy, allowing for an application efficiency of between 60 and 85% (Sandoval-Solis et al., 2013; Yonts, Kranz, & Martin, 2007). Low Energy Precision Application (LEPA) is a pivot irrigation technology where low-pressure sprinklers (less than 6 psi) are placed no more than one foot above the soil. This design has increased application efficiency to 95% (Amosson, New, Bretz, & Marek, 2001). Advances in precision irrigation have allowed growers to differentially water separate sections of the field, depending on irrigation requirements, so that each section receives only as much water as is necessary (Sadler, Evans, Stone, & Camp, 2005). Regardless, pivot irrigation still requires an adequate water source and exposes foliage to extended leaf wetness and the risk of foliar diseases (Turkington, et al., 2016; Aegerter, et al., 2008).

Drip or micro-irrigation can be more efficient in water use on the field scale, but it can also be more expensive and may actually lead to greater water use if not correctly applied. Originally, micro irrigation was utilized in small-scale production systems (Camp, 1998; Devasirvatham, 2009; Lamm, 2002). As long as 4,000 years ago, in many parts of the world (including Africa, China, southern Asia and Native American tribes in North and South America), large, unglazed round clay pots with a small opening, commonly known as ollas (Figure 2.2), were buried in the soil and filled with water to irrigate fields (Bayuk, 2010). The ollas would slowly seep out water through the porous, terracotta clay into the soil.

Modern drip tape irrigation was invented in Israel in 1965, by Simcha Blass of the Netafim Company, and it was first sold in 1966 for use in vineyards in the Negev desert (Shamah, 2013; Netafim, 2015). The principle of drip irrigation is that water is applied directly to the root zone, either on the soil surface or from driplines buried below the soil surface. Drip irrigation has been shown to reduce water loss through evaporation, increase water use efficiency to between 90-95%, (Lakew, Anteneh, & Ayalew, 2014), and increase yields (Camp, 1998; Devasirvatham, 2009; Lamm, 2002). Lamm & Troien (2003) reviewed ten years of research at Kansas State University and reported that subsurface drip irrigation can reduce water use by 35-55% in corn. In a study on the effects of water subsidies on agriculture in the lower Rio Grande irrigation districts, Ward and Pulido-Valazquez (2008) reported data for the use of water in drip irrigation and flood irrigation. On a scale of acre-feet per acre per year, farmers using flood irrigation usually applied 0.9 to 2.8 more acre-feet of water as growers of the same crop using drip irrigation in 2006 (Ward &

Pulido-Velazquez, 2008). Interestingly, they reported that subsidized drip irrigation may increase overall water use because more growers would be incentivized to use drip irrigation, less water would be returned to groundwater or return flows for downstream delivery, and greater yields may actually increase crop evapotranspiration (0.2 to 0.7 acre feet greater evapotranspiration of drip irrigation over flood irrigation) (Ward & Pulido-Velazquez, 2008). They suggest that this technology be used in addition with other strategies, such as deficit irrigation or the intentional reduction in irrigation amounts to conserve water and improve crop quality.

Drip irrigation can be more expensive than other forms of irrigation due to the extra cost of equipment (drip tape, emitters, extra pipe, installation equipment) and replacement of drip line in annual crops (Devasirvatham, 2009; Lamm, 2002). Ward & Pulido-Velazquez (2008) reported the cost of drip irrigation in their study area was between $113 (for grain sorghum) and $3,086 (for fall onions) greater than furrow irrigation per acre-year. Cost tends to be the most limiting factor in deciding whether to use drip irrigation in low value crops where water use is not as restrictive. In high value crops such as vegetable crops, the cost may be made up.

Drip irrigation can also lead to significant salt buildup if either the soil is not sufficiently flushed from time to time, the water is high in soluble salts, or both (Burt & Isbell, 2005). As water evaporates from the soil surface, these salts remain in the soil, whereas, with irrigation techniques such as flood or furrow, deep percolation would allow for salts to be leached below the root zone. Drip irrigation does not normally allow for soil leaching of salts deposited with tap or well water use, yet

(Burt & Isbell, 2005) demonstrate that salts can be leached from the soil when the irrigator applies excessive water sufficient to cause deep percolation.

Despite its greater efficiency, drip irrigation is still the least used irrigation strategy in the US, accounting for only 4.61 million acres or 7.4% of all irrigated land in 2010 (Maupin M. , Kenny, Hutson, Lovelace, Barber, & Linsey, 2014). In California, it is the second most utilized irrigation strategy at 39% of all irrigation in 2010, possibly because of the high value of crops and efforts to increase water efficiency (Tindula, Orang, & Snyder, 2013).

Irrigation management strategies

Aside from the method of irrigation, it is also important to consider irrigation timing and frequency when reducing water use. The goal for efficient irrigation is to apply water only when it is needed to produce yield profitably and reduce drought stress. A number of methods have been developed to assess soil and crop water status to avoid permanent wilting point and maintain plant growth. One such method has been to estimate the amount of water used by crops on any given day by measuring the environmental parameters that affect water loss. Crop evapotranspiration (mm per unit time, usually hour or day) estimates are calculated for any crop by the following formula:

$$ET_c = K_c(ET_o)$$

where ET_o is the evapotranspiration of a reference crop and K_c is the crop coefficient. Reference crop ET is usually measured experimentally based on two well-watered crop types: a short crop such as turf grass and a tall crop such as 0.5 m alfalfa (Snyder, Orange, Matyac, & Eching, 2001; Itenfisu, Elliott, Allen, & Walter, 2003).

Several formulas and methods have been developed to estimate ET_o (See Jensen & Allen (2000) for a full history). The most popular method is the modified Penman-Monteith equation (Equation 2.1), which includes factors that influence water loss, such as saturation vapor pressure, temperature, and wind speed. This equation also considers factors that affect water loss from the soil, such as net radiation soil heat flux (Snyder, Orange, Matyac, & Eching, 2001).

The crop coefficient is a ratio of crop evapotranspiration to reference ET_o, and it is specific to certain crops grown under specific conditions (i.e. climate, soil type) and dependent on crop stage. Measurements of K_c are made by using experimental plots and either direct measurements (e.g. lysimeters) or indirect measurements (e.g. meteorological data and models) (Allen et al. 1998).

Evapotranspiration estimations are often used as a benchmark for water use by crops, and it is calculated by state governmental and educational institutions for the public. Evapotranspiration estimates by region and crop coefficients are often broadcasted on radio or available on the internet via the California Irrigation Management Information System, CIMIS (California Department of Water Resources, 2016) Growers can use these values to set irrigation scheduling to avoid overwatering. Many drought studies also use evapotranspiration estimates as the well-watered control standard in lieu of soil water saturation. Also, deficit irrigation schedules as well as drought treatments are often set as a percentage of this estimation.

In spite of its usefulness as a guideline, there is much variability in crop ET estimates because they are measured using specific conditions at regional weather stations. Alternatively, measurements of soil and plant water status have been used to determine when plants are sufficiently stressed and require irrigation. Soil moisture in the field can be monitored using water moisture sensors, such as dielectric moisture sensors, gypsum block sensors, or tensiometers. Dielectric sensors exploit the electrical conductivity of water by measuring the dielectric permittivity or the ability of water to store electrical charge in a magnetic field (Morris, 2006). Gypsum block sensors measure the electrical resistance within a porous substance, such as gypsum, as it loses or gains water content (Morris, 2006). Tensiometers work by measuring the negative tension created by a vacuum as water is drawn out of the tensiometer tube through a porous ceramic tip at the bottom end in drying soil (Tasmanian Government, 2007; Morris, 2006)

A neutron probe is another apparatus for measuring water content of the soil. It works by emitting high-energy neutrons from Americium 241/Beryllium in the soil. High-energy neutrons interact with hydrogen ions, lose energy, and are sensed by a neutron sensor. Water is the largest hydrogen-carrying component of soil, so changes in soil water content can easily be detected by this method. It is also more accurate over a larger area of the soil. However, since soil organic matter is also hydrogen rich, the probes must be calibrated to the soil type. Neutron probes must be inserted into an access tube and the detector must be at least six inches below the soil surface to avoid neutron loss to the air. They also require special training and licensing because of the radioactivity. This makes them impractical for use by most commercial growers (University of California, 2016).

Midday stem water potential (SWP) has also been employed to schedule irrigation, especially in perennial crops, and it can provide more accurate assessment of water stress (Shackel, et al., 1997). The water potential of plants is closest to the soil water potential just before dawn and slowly decreases throughout the day. Generally, water potential becomes lower the further from the soil-root interface the plant organ, and this creates the water potential gradient responsible for transporting water through the plant. Midday stem water potential is an accurate measure of the water stress of a plant. Predawn stem water potential is an estimate of the soil water potential. Water potential is measured in leaves by covering the leaf to be measured for a couple of minutes to reduce transpiration and water loss from the tissue, which would skew the measurement. The leaf is then excised and sealed in the pressure chamber, also known as a pressure bomb, with the cut end flush with the top of the rubber seal. Pressure is then applied to the chamber until xylem sap can be seen just starting to exude from the cut end. At this point, the pressure applied to the leaf is equal to the inverse of the total water potential of the leaf tissue (Scholander, Hammel, Hemmingsen, & Bradstreet, 1964).

Maximum daily trunk shrinkage (MDS) has also been used as a proxy for midday stem water potential because of its greater convenience and strong correlation to several drought stress parameters. Stem water potential measurements must be taken manually in a one-hour window (usually 1-2 pm), but

MDS can be measured automatically at regular intervals through the day, reducing measurement error and increasing efficiency (Goldhamer, et al., 2003). MDS measurements are obtained by a linear variable differential transformer (LVDTs; Figure 2.3) that is permanently drilled into the trunk (or major scaffold branch) of a representative tree and attached to rubber belts that surround the trunk. LVDTs use magnets surrounding a moveable metal core under tension (usually nickel iron) to transmit change in position of the core from a neutral position (reflecting change in diameter) to an electrical signal (Macro Sensors (TM) , 2014). This signal can be collected by data loggers and transmitted via cell phone or internet to the grower (Goldhamer, et al., 2003).

In almond tree irrigation research, Goldhamer et al. (2003) found that MDS is correlated to Vapor Pressure Deficit in thoroughly watered trees and to midday SWP in drought stressed trees. They used MDS measurements with two established thresholds (1.75 and 2.75 mm) to determine when best to irrigate almond for good harvest results balanced with reduction in water use. Irrigation was adjusted in their experiment every three days based on MDS signals. They lowered the irrigation by 10% if the MDS did not exceed the threshold and raised it by 10% if it did. Irrigation was managed this way throughout the growing season. Nuts were harvested from each treatment block as well as from an adjacent orchard on the same property irrigated by the growers traditional SWP based irrigation schedule.

Goldhamer et al. (2003) found that reduced irrigation based on MDS thresholds increased desirable qualities of almonds (e.g. rate of hull splitting), kernel desiccation, and percent kernel. An increased hull split allows the almond to dry more thoroughly on the tree, reducing ground drying time, ant damage, and fungal contamination (Goldhamer, Fereres, & Salinas, 2003; Zalom & Bentley, 1985). Decreased kernel hydration is desirable for texture and storage as it allows for decreased rot incidence. Differences in gross yield were minimal and not significantly different. There were also no significant difference in either fresh or dry kernel and whole nut weight between the 1.75 threshold treatment and the control, while the 2.75 threshold treatment differed by less than 12% in all categories from the 1.75 treatment. Goldhamer et al. (2003) reduced water use from the grower's standard by 4.5% using the 1.75 threshold and 41.5% using the 2.75 threshold.

The method of irrigation scheduling employed by Goldhamer et al. (2003) has come to be known commonly as Deficit Irrigation (DI). There are two general types of deficit irrigation, regulated deficit irrigation and partial root zone drying (PRD) (Costa, Ortuña, & Chaves, 2007), also known as Controlled Alternate Partial Rootzone Irrigation. Regulated deficit irrigation is the practice of applying irrigation based on the water status of the crop. This is determined by either stress indicators, such as ET estimates or direct measurements like soil moisture, SWP and MDS, or by the phenology of the crop. Using stress indicators involves monitoring crop stress and applying water only when a determined threshold is reached, like in the case of Goldhamer et al. (2003). When applying irrigation using phenological cues, increased water is applied when used by the plant toward desired growth parameters and irrigation is reduced during periods of undesirable growth (Costa, Ortuña, & Chaves, 2007).

Early research in fruit trees, such as peach, pear and apple, in Australia showed that events that contribute to yield, such as flowering, fruit set, and development, take place in the first and third phase of the growing season. But excessive shoot growth, an undesirable growth parameter, takes place in the middle third of the growing season (Kriedemann & Goodwin, 2002). They showed that stone and pome fruits that successfully set by the end of phase 1 grew slowly during phase 2, competed less with growing foliage for photoassimilates, and were less sensitive to water stress than foliage and shoot growth. In the third phase of the growing season, fruit experiences rapid expansion, and it was beneficial to resume normal irrigation levels (Kriedemann & Goodwin, 2002). By withholding water during the second phase, they were able to limit canopy density. Kriedman & Goodwin (2002) point out this has three main advantages: increased fruit bud initiation, increased sunlight penetration, and reduced transpiration. Floral bud formation is influenced by a number of conditions both genetic and ecological. However, in many cases, shoot growth and floral induction are often at odds with each other (Koutinas, Pepelyankov, & Lichev, 2010). This is possibly due to competition for carbon resources, opposing hormonal signals or both, and floral bud formation increases with more light exposure in several perennial plants (Wilkie, Sedgley, & Oleson, 2008). Increased sunlight penetration allows for existing foliage to absorb more direct sunlight, an objective usually met by aggressive pruning. In Bartlett pears, Mitchel et al (1989) found that weight of requisite summer prunings was positively correlated with irrigation level. Transpiration in many of the cases was reduced by a third because there was simply less foliage in the Regulated Deficit irrigated trees and stomatal conductance was reduced in response to ABA signals from the drying soil. These last two responses are typical of minor drought-induced responses.

Regulated deficit irrigation can be successfully applied to annual crops as well. In maize, Farré & Faci (2009) found that stress imposed by increasing irrigation intervals in any stage other than tassel emergence to milk stage increased irrigation water use efficiency measured as "the ratio of grain yield to total irrigation water applied," compared to the fully irrigated corn plots. They showed that plots fully irrigated during tassel to milk stages, but with stress imposed during vegetative stages or both vegetative stages and grain fill (milk stage to physiological maturity) had minimal yield impacts. However, these regimes did however show a reduction in irrigation by about 45% and 25%, respectively. Interestingly, the former treatment showed the least reduction in grain yield from the thoroughly irrigated treatment of all deficit treatments, 86 g-m^{-2} in the first year and 124 g-m^{-2} in the second year of the study (Farré & Faci, 2009).

In partial root zone drying, water is applied to one side of the root zone while the opposing side is allowed to dry out until stress conditions are met, then the side of irrigation is switched (Kriedemann & Goodwin, 2002; Sepaskhah & Ahmadi, 2010). This method imitates the natural process of soil drying from the upper layers to lower layers. When used with drip irrigation or microsprinklers, partial root zone drying may be more expensive because two lines are required per row with separate shutoff valves. However, initial costs may be offset if improved water use efficiency results in sufficient water savings. Partial root zone drying can also be used in furrow irrigation if designed so that alternating furrows can be watered at different times.

Like regulated deficit irrigation, partial root zone drying exposes roots to drying soil. By simultaneously keeping one side of the root zone well hydrated, roots on the drying side of the root zone produce drought signals, while roots on the irrigated side can potentially maintain adequate crop hydration. Studies have shown that plants under partial root zone drying have increased ABA production and translocation to leaves (Kang & Zhang, 2004; Kudayarova, Vysotskaya, Cherkozyanova, & Dodd, 2007; Liu, Shahnazari, Andersen, Jacobsen, & Jensen, 2006b), increased xylem pH, and decreased cytokinins (Costa, Ortuña, & Chaves, 2007; Kudayarova, Vysotskaya, Cherkozyanova, & Dodd, 2007). These factors influence stomata in leaves to close, reduce shoot growth, and maintain root growth on the drying side of the plant. Research has also shown that crops rapidly take water up after drought and hydraulic conductivity is improved in roots previously exposed to minor drought (Kang & Zhang, 2004). However, roots exposed too long to drying soil become impermeable to water penetration (suberized) (North & Nobel, 1991) This can potentially result in a collapsed cortex and reduced secondary root growth. Thus, it is advantageous to allow roots to be exposed to soil drying conditions long enough to benefit from the effects of minor drought conditions without creating permanent damage. However, some studies have shown that fixed irrigation sides without alternating irrigation can be more efficient under specific and limited conditions (Sepaskhah & Ghasemi, 2008). Drought stress is usually monitored here by assessing soil water content or potential, since trunk shrinkage and stem/leaf water potential can be affected by the hydration of the irrigated side of the rootzone (Egea, Dodd, González, Domingo, & Baille, 2011).

In many cases, leaf water potential was not significantly lower in plants under partial root zone drying than those watered across the whole root zone. In tomatoes, (Kudayarova, Vysotskaya, Cherkozyanova, & Dodd, 2007) found that plants watered at half the rate of the well-watered controls on alternating sides had less than or equal to a 0.1 MPa, or 1 bar, difference in midday (10-12 am) leaf water potential, which is relatively small difference. Zegbe, et al., (2005) found that leaf xylem water potential water potential was not significantly lower in tomatoes subjected to partial root zone drying, except during later phenological stages, and never exceeded -1.2 MPa, which is considered to be mild stress (Bostock, Pye, & Roubtsova, 2014). In almond trees, (Egea, Dodd, González, Domingo, & Baille, 2011) found that partial root zone drying improved water status and reduced daily trunk diameter fluctuations compared to trees under regulated deficit irrigation.

Both regulated deficit irrigation and partial root zone drying have shown consistent results in increasing water use efficiency and improving crop quality with minimal and sometimes no reduction in yield.

Table 2.1 is a summary of some of the research done on various crops irrigated by regulated deficit irrigation or partial root zone drying. Most stone and pome fruit in early regulated deficit irrigation research was not statistically smaller than the fruit from fully irrigated fruit and some researchers found that fruit actually increased in size compared to trees watered fully throughout the season (Jerie, Mitchell, & Goodwin, 1989). This was not the case in grapes where deficit irrigation imposed in the late season produced smaller berries. However, studies in grape vines have shown improved quality of grapes under regulated deficit irrigation regulated deficit irrigation (Kriedemann & Goodwin, 2002). In contrast, Kriedemann & Goodwin, (2002) reported that partial root zone drying studies on grape increased grape size compared to regulated deficit irrigation and control irrigation.

In mangoes grown in the dry season in Thailand, (Spreer, Nagle, Neidhart, Carle, Ongprasert, & Müller, 2007) demonstrated that Partial root zone drying increased fruit size, sugar content, and the edibility of mangoes with minimal yield reduction and increased water use efficiency (Table 1). Wahbi, et al. (2005) reported findings of increased water use efficiency under partial root zone drying, but did not find statistically different oil content or acidity.

In potatoes, Liu, et al. (2006b) found that partial root zone drying irrigation (70% of full irrigation switched every 5-10 days) actually yielded around 11% more biomass than the fully irrigated while using 30% less water. Earlier the same year in potted experiments, (Liu, et al. 2006a) found that partial root zone drying at 50% of full irrigation had a slightly less water use efficiency, while 50% deficit irrigation applied evenly over the season yielded a significantly greater water use efficiency. This suggests that for potatoes, partial root zone drying may be more efficient at lower irrigation levels. Shamzari et al. (2007) followed up this research with another field experiment applying partial root zone drying at 70% and found similar results as Liu et al. (2006b in review by Sepaskhah & Ahmadi, 2010).

Some studies suggest that there is a more pronounced difference in yield between deficit irrigation and partial root zone drying in drier years with greater crop water demand (Leib, et al., 2006; Spreer, et al., 2007; Caspari, et al., 2004). In their paper on deficit irrigation in mangoes, Spreer, et al., (2007) compared partial root zone drying and partial root zone drying irrigation strategies and reported a roughly 2.8-3.5-fold greater yield loss in partial root zone drying compared to partial root zone drying. From 2001-2003, Leib et al. (2005) studied the effect of deficit irrigation and partial root zone drying on Fuji apple trees in eastern Washington state. The researchers aimed at irrigating regulated deficit irrigation and partial root zone drying treatments between 50% of the control irrigation treatment for the first year and second years but found it necessary to adjust partial root zone drying treatments to 60% of control irrigation in the third year to maintain the wet side at field capacity at all times. This required additional irrigation time when changing the side of the root zone to be irrigated (Leib, et al., 2006). Deficit irrigation treatment was also adusted to 60% in the third year for consistency. Control irrigation was set to maintain field capacity as much as possible and so was 60-70% of Crop evapotranspiration. With few exceptions, the soil moisture content and soil water potential were higher in at least one side of the root zone of partial root zone drying treated trees as compared to the deficit irrigation treated trees entire root zone. Deficit irrigation yielded the lowest amount of apples in fruit weight per tree among all years and the lowest average fruit size in all years but 2002, while PDR treatment affected yield and size to a lesser extent. In 2002, the yield from deficit irrigation treated trees was lower than control irrigation, but not partial root zone drying. Partial root zone drying trees did not significantly differ from any other treatment in all three years. In year three, there was actually a higher yield of apples in the partial root zone drying treatment than in any of the other years despite higher cumulative Crop evapotranspiration and lower rainfall. This study found that the Brix value, indicating soluble solid concentration, including sugars, was generally highest in deficit irrigated apples and intermediate in PDR apples with significant differences between deficit irrigation and control irrigation. Apple firmness varied between years and days after harvest; however, neither deficit irrigation or partial root zone drying treated apples were firmer than control irrigation apples. Partial root-zone drying treated apples tended to gain firmness with age across all years while apples from the other two treatments lost firmness in 2001.

Partial root zone drying may also have a more positive effect on root growth than partial root zone drying. Abrisqueta et al. (2008) studied the root dynamics of young peach trees under deficit irrigation. The entire root zone was watered with 50% crop evapotranspiration compared to a control (100% crop evapotranspiration), and alternating root zone drying on a two to three week schedule. A Minirhizotron™, a scanning digital camera fitted in a plexiglass tube, was inserted via a soil corer at a 45° angle into the ground 0.5 meters from the first drip emitter from the trunk of the tree. With this technology they measured root density and growth rate of roots growing along the tube at various depths from the surface to one meter deep. They also measured the growth rate of feeder roots in response to each treatment and found that root growth was inhibited by only 43% in the partial root zone drying treatment as compared to 73% in the Deficit irrigation treatment. Partial root zone drying treatment utilized 53% of the water and deficit irrigation treatment utilized 44%.

Ideally, it is best to irrigate crops to increase yields or optimize profits. When faced with water shortages, though, this is not always possible. Without a plan to budget water usage, a grower is faced with the possibility of fallowing fields, destroying orchards that required significant investments in time and money, or facing devastating losses in yield. Alternatively, with proper planning, water saving strategies, such as deficit irrigation and efficient application methods, can increase water use efficiency to salvage cropyields inspite of water shortages.

Cover crops and soil organic matter management

Water management can also be manipulated through soil management practices. Depending on the texture of the soil, water may be easily lost to deep percolation and evaporation in the case of sandier soils or held tightly by soil in the case of clay soils. This can reduce plant water availability even when there is sufficient water content. Proper soil texture and structure ensure that water holding capacity and plant water availability of soil is optimal, and allows soil to absorb and retain as much water applied as possible.

An important component of soil structure is soil aggregation. Since soil texture is not easily changed, soil aggregation is best achieved practically by maintaining organic matter content and disturbing the soil as little as possible. Organic matter has many advantages to soil ecosystem, including improved soil nutrition, increased microbial activity, and reduced soil erosion and weed competition when applied to the soil surface (Lewandowski, 2014). In terms of water holding capacity, Soil organic matter SOM aids in the formation of micro- (<250 μm) and macroaggregates (>250μm), between which form transmission (>50μm) pores that allow free movement of water and storage pores (0.5-50 μm) that retain water and release it to plants (Chen & Avnimelech, 1986).

When thoroughly decomposed by microbial activity, SOM is converted to humic materials that form complexes with clay particles by various means, including Van der Waals forces and covalent and electrostatic metal bridges. Humic materials can also form netlike structures that aid in binding silt and sand particles (Chen & Avnimelech, 1986). At any stage of decomposition, organic matter itself is also very porous and absorptive, and it can increase available water capacity in all soil textures (Hudson B. D., 1994; Rawls, Pachepsky, Ritchie, Sobecki, & Bloodworth, 2003).

When applied to the soil surface as residue, organic matter can reduce evaporation from the soil surface. Residue covered corn plots had reduced evapotranspiration and increased water content throughout most of the season compared to bare soil corn plots irrigated at the same rate (van Donk, Martin, Irmak, Melvin, Peterson, & Davidson, 2010; Sarrantonio, 2007). Soil organic matter can also physically protect soil from wind and rain erosion, prevent crust formation in heavy clay soils and increases water infiltration into the soil (Grant, Anderson, Prichard, Hasey, Bugg, & Thomas, 2006)

Addition of organic matter to the field, orchard, or vineyard is achieved either by application of dried plant matter, such as straw or mulch, composted material or manure, leaving residue in the field from previous crops, or by growing cover crops (Cooperband, 2002). An important consideration when leaving residue is disease management. Inoculum from residue borne diseases, or foliar/stem diseases, left on the field from the previous season could easily infect current season crops unless: 1) they are non-hosts, or 2) the residue is removed, destroyed or tilled under the soil surface to be decomposed (Bockus & Shroyer, 1998). Residue removal will diminish the advantages of adding organic matter as mulch. Alternating the field to a non- host may avoid this problem, but this is only feasible in annual cropping systems (Bockus & Shroyer, 1998).

Bulk addition of mulch is easy to apply, but may be prohibitively expensive on large acreages except for use in high value crops. Organic mulch in the form of hay can be much cheaper than plastic ranging in price of $75-$300 per ton (USDA, 2016). Synthetic mulches like plastic coverings or reflective mulch has been used for greater than 30 years in high value crops like strawberry and tomato in California. (Mitchell, Summers, McGriffin, Aguiar, Aslan, & Stapleton, 2004). These mulches do maintain soil moisture for soils irrigated by subsurface drip, but they do not allow much penetration of above ground precipitation, and they can even increase runoff from rain events (Smith, et al., 2015). They are also among the most expensive mulch types, ranging in cost from $200 to $700 dollars per acre per growing season (Shrefler & Brandenberger, 2014; Hannan, 2011; Schrader, 2000).

Planting cover crops is an alternative to bulk addition of mulch that may be more inexpensive, if the cost of seed is cheaper than the cost of the mulch. Fuel expenses could be considered similar for spreading and planting operations. Despite the benefits of growing cover crops, they are rarely used in arid and semi-arid regions of California. One of the most prohibitive reasons for not using cover crops is the possibility that cover crops will use more water than they can save in semi- and arid regions. Like any other crop, cover crops do require water to establish and grow. If sufficient winter precipitation does not occur, as is the case in drought years, or cover crops are grown too close to or in conjunction with a cash crop, then cover crops may compete with cash crops for soil moisture. In a review of the data on water use in cover crops, Unger & Virgil (1998) concluded that cover crops are more suited to humid and sub-humid regions where precipitation is adequate to support cover crops without impacting cash crops significantly. A number of studies have shown that cover crops can reduce the amount of water available to cash crops at the time of planting (Nielson, et al., 2015; Nielson & Vigil, 2005; Zhu, et al., 1991; Mitchell, et al., 1999). Studies in the semi-arid region of western Nebraska and eastern Colorado by Nielson & Vigil (2005) and Nielson et al. (2015), showed that cover crops could significantly reduce wheat yields by reducing soil water availability at the time of planting, even though Nielson et al. (2015) found that cover crops of single and mixed species increased precipitation storage efficiency, measured as a percentage of precipitation lost to runoff.

However, utilizing normal or above normal winter precipitation to establish biomass for SOM in non-drought year may buffer soil water loss during the dry season and can be a strategy to capitalize on wetter years. Most of the studies mentioned show that once terminated, cover crops act as mulch and increases water storage capacity (Nielson, et al., 2015), preventing evaporative loss and increasing water infiltration much in the same way crop residues and manually added mulch. Studies in California (Joyce, et al., 2002; Smith, et al., 2015) show that cover crops increase infiltration of water during rain events both while growing and as long after termination as residue remains on the soil surface. In a two year study in the Sacramento Valley, (Joyce, et al., 2002) found that farming practices that incorporated cover crops in lieu of fallow ground in a four year rotation had significantly less runoff during rain events and equal or greater volumetric soil water content than conventional fallow rotation by the end of the rainy season in all but a few cases, indicating that cover crops could be advantageous to conserve precipitation during wetter winters. In their study winter cover crops (December to March) were planted in conventional, low input, and organic plots in four-year rotations of tomato, safflower, corn followed by winter wheat then bean. Conventional plots were fallowed in winter months except when planted to winter wheat. In contrast to this, the low input and organic plots were kept planted year round and included cover crops of oat and purple vetch or common vetch. Low impact and organic plots also showed ca. 85% less runoff in 2000 and 60% to 76% less runoff in 1999 than conventional plots, respectively. Soil hydraulic conductivity was also greater throughout the winter of 1999-2000 in plots with cover crops.

In contrast to growing cover crops to maturity, low residue cover cropping is a system that is currently being advocated as a short season strategy to increase water infiltration and increase SOM during winter months, especially in vegetable fields where farmers cannot afford to grow cover crops for long periods of time. (Smith, et al., 2015). This strategy employs fast growing cover crops, such as rye or triticale, during the off-season and allowing this cover to grow for approximately 60 days or until it has reached 10-20% of its biomass (Smith, et al., 2015). The cover crop may be allowed to grow longer if desired, but then may interfere with tilling practices. In specialty crops, tillage is still the most preferred method of weed control. Work in the Salinas Valley along the central coast of California by the University of California and USDA has shown that this strategy can reduce water loss from rain events by 96,541- 114,023 gal per acre (or about 3.55 to 4.2 inches of rain over the winter of 2010-2011) (Smith, et al., 2015).

It may be that, in order for cover crops to be a useful tool for water conservation, they should be considered when winter precipitation is forecasted to be average or greater than average, and that they be grown long enough to produce enough biomass to adequately cover the soil surface or increase soil carbon content to increase water infiltration and storage capacity.

In perennial woody systems such as vineyards and orchards, cover crops may be grown during dormancy. For example, between leaf drop to bud burst, cover crops do not compete with dormant perennials. However, ground cover does utilize soil water that can be used at bud break, and thus, can increase overall water requirements (Grant, et al., 2006; Ingels, van Horn, Bugg, & Miller , 1994). Ground cover crops can also interfere with radial heating from the ground that may make expanding buds susceptible to frost damage in late winter early spring, and it also may harbor ice-nucleating bacteria (Ingels, et al., 1994; Snyder & Paulo de Melo-Abreu, 2005). Snyder & Paulo de Melo-Abreu (2005) suggest cutting or removing traps crops far enough in advance to allow the residue to decompose before spring.

However, they argue that tall cover crops that are not mowed can be utilized as a substrate for undertree sprinkler-mediated latent heating to prevent freeze damage. A common frost protection method used in orchards in the western US is the use of under tree sprinklers that releases heat as it freezes. If possible, warm water is applied to prevent the air temperature from dropping too far initially and increases the effect. The amount of frost protection depends on the temperature of the water and the amount of water applied. The ground cover provides a greater surface area on which water can be deposited and evaporated (Evans, 1999; Anconelli, et al., 2002). Though many agricultural areas of California are located in regions where temperatures rarely drop below freezing, frost events following winter storms occur infrequently. Logistic issues must also be considered when growing cover crops in nut orchards because harvesting in nuts requires a “clean” orchard floor for nut drying mechanical sweepers.

The key to increasing irrigation efficiency lies not only in improving application efficiency, which is important in itself, but also in understanding how water is used by plants and flows through the soil-plant-atmosphere continuum. Managing irrigation timing and amount can allow the grower to manipulate this flow of water to increase the water use efficiency of the crop itself. This may reduce yield below optimum; however, this loss is usually not very large. In the case where water access is severely restricted due source depletion or water policy, reduced yield per plant is better than no yield or the possibility of fallowing fields or destroying orchards that died. Other benefits may also be realized under proper deficit irrigation such as improved yield quality and reduced labor cost, such as in pruning time requirements.

Figure 2.1. Original center pivot invented by Frank Zybach (Gaines, 2015)

Figure 2.2 Olla (left) made by the Cahuilla Indians of Southern California (Hunter, 2016)

Figure 2.3. Linear variable differential transformer (LVDT; Goldhamer et al., 2003)

Table 2.1. List of selected references on deficit irrigation studies

Year	Crop	Method of irrigation	Water use	WUE	Yield loss/Biomass reduction	Source	Notes
1984	Beans	PRD (AFI)	22-29% reduction	---	9-38% reduction **	Samadi and Sepaskhah (1984)	** Smaller reductions were seen when supplemental irrigation in all furrows was applied at pod fill stage.
2006	Cotton	PRD (AFI; 22.5, 30, and 45 mm)	Same amounts were applied to all treatments but reported 30-60% less than normally practiced in the area.	3.83-24.42% increase depending on year and irrigation level	12.8-24% increase depending on year and irrigation level	Du et al. (2006)	Compared deficit irrigation with PRD and found yields and WUE to be greater in PRD.
2001	Hot Peppers	PRD	40% reduction	61.5%-77% increase (g/kg yield)	3.5% decrease to 3.4% increase compared to even watering	Kang et al. 2001	Laboratory conditions in which plants were grown n pots at 65% and 55% field capacity. Root to shoot ratio was increased compared to even watering or fixed irrigation to one side of the rootzone.
1997	Maize	PRD	35% reduction in water use		6-11%	Kang et al. 1997	Researchers found anatomical differences in drying roots
2002	Maize	Vertical PRD	20%-40% reduction	21-41% increase over surface irrigation	12-17.6% decrease in biomass	Kang et al. 2002	NotablyIncreased Nitrogen and Potassium uptake in alternated watering.

2007	Mango	PRD and RDI	51% to 46% reduction in PRD and 49-35% in RDI	29%-36% increase in PRD and 14%-15% increase in RDI	3.8%-10% in PRD and 14%-28% in RDI	Spreer et al. (2007)	Increased fruit quality in both RDI and PRD treatments and increased size in PRD
2005	Olive	PRD	---	57%-70% increase when irrigation was switched every four weeks 62.5%-78.5% increased when irrigation was switched at each event.	10.6%-19% reduction when irrigation was switched every 4 weeks and 15%-22.5% when irrigation switched at each watering event.	Wahbi et al. (2005)	
2006	Potatoes	PRD (70% of full irrigation)	30% reduction	60% increase	11% increase	Liu et al.(2006b)	A pot experiment in another study by the same authors showed 50% irrigation level to have significantly greater reductions in yield.
2007	Potatoes	PRD (70% of full irrigation)	30% reduction	61% increase	20% increase	Shahnazari et al. (2007)	
2006	Raspberry	RDI	Reported 75% reduction in water use without negative effect on yield or quality.	Increases reported in graph form only	8% increase to 27% decrease; most treatments were between 3 and 15% difference.	Koumanov et al. 2006	

2008	Sorghum	PRD (Alternate furrow irrigation AFI) at 10, 15 and 20 day interval switches.	26-27.3% reduction in applied water switched at 10 day intervals	12.3% increase in water use efficiency (10 day intervals*)	19% to 21% (10 day interval)	Sepaskhah and Ghasemi (2008)	*Difference in WUE and yield increased with greater intervals between furrow irrigation change. WUE was consistently lower in fields where both furrows or only every other furrow were irrigated without switching. Deep percolation was also reduced in alternate furrow irrigation.
2004	Tomato	PRD	50% reduction			Kirda et al. (2004)	Greenhouse conditions
2008	Winter wheat	PRD (AFI)	41% reductions	32-41% increase	15% reduction	Sepaskhah and Hosseini (2008)	Found a greater protein content under PRD
Partial root zone drying PRD, Regulated deficit irrigation RDI, Alternate furrow irrigation AFI							

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Chapter 3 Pest Interactions with Water-Stressed Plants

Maintaining proper irrigation is not only important for conserving water and increasing water use efficiency, it also influences the crops ability to withstand disease and pest pressure. There are different lines of thought on the effect of poor irrigation practices on diseases and pest performance in plants. Adequate watering prevents stress that can attract insect pests and/or weaken the plants response to insect herbivore or disease attack. In addition, stressors may affect the immune responses of plants by stimulating expression of defense related genes. It is likely that all these factors interact for different disease or pest conditions due to the diverse strategies employed to attack plant hosts. It is important to recognize how water stress can negatively or positively affect a crops ability to defend itself.

Drought stress and its effects on disease development

Plant pathogens rely on their ability to subvert plant defenses or appropriate host metabolic pathways for successful infection and reproduction. In response to pathogen attack, plants utilize a number of phytohormones that signal the expression of pathogenicity related genes in response to damage caused by pathogens or chemicals exuded from the pathogens, known as pathogen-associated molecular patterns or microbe-associated molecular patterns (Pieterse, Does, Zamioudis, Leon-Reyes, & Wees, 2012). These phytohormones, including abscisic acid (ABA), jasmonic acid, salicylic acid, ethylene, and reactive oxygen species (ROS; like H_2O_2 and NO), also play an integral part of drought stress signaling and adaptation, and they are expressed in response to some diseases and insect attack sand other stress signals.

The interaction of these phytohormones and their regulation in response to multiple stressors is complicated and not fully understood (Pieterse, Does, Zamioudis, Leon-Reyes, & Wees, 2012; Bostock, Pye, & Roubtsova, 2014). Traditionally, it was accepted that drought predisposes plants to disease infection. For instance, the effect of drought as a catalyst for outbreaks of *Armillaria mellea* in forests has been reported by a number of studies (Desprez-Loustau, Marçais, Nageleisen, Piou, & Vannini, 2006). However, evidence shows that the interaction between these phytohormones cause pathogens to respond differently depending on the mode and location of infection. For instance, canker diseases caused by necrotrophic fungi that attack the cambium of woody perennials are aggravated by drought stress. In raywood ash trees following drought stress, *Botryosphaeria stevensii* cankers grow larger than in non-stressed trees (Bostock, Pye, & Roubtsova, 2014). Almond trees with lower stem water content are more susceptible to *Fusarium acuminatum* cankers (Marek, Yaghmour, & Bostock, 2013). In contrast to this, powdery mildew (*Oidium neolycopersici*; a biotroph) infections were found to be reduced in drought-stressed tomato plants compared to the control or salt stressed plants (Achuo, Prinsen, & Höfte, 2006). This response was accompanied by increases in abscisic acid levels within the leaf. Vascular wilt incidence in alfalfa caused by *Verticillium albo-atrum* was found to be greater in plots watered at higher rates, and a linear increase was found between disease symptom incidence and irrigation level (Jefferson & Gossen, 2002), whereas in hardwood trees such as

Acer spp., drought stress is correlated with dieback and even mortality caused by Verticillium wilt (Berlanger & Powelson, 2000). Bostock, Pye, & Roubtsova (2014) wrote a comprehensive review of the interactions between phytohormones, their role in drought stress, and predisposition to disease.

Role of jasmonic acid in drought stress and defense signaling

Jasmonic acid is a hormone involved in insect and disease defense and derived from the fatty acid α-linoleic acid. It is easily metabolize to methyl jasmonate or amino acid conjugates, such as Jasmonyl-Isoleucine (JA-Ile) (Pieterse, Does, Zamioudis, Leon-Reyes, & Wees, 2012). Ollas, Hernando, Arbon, & Gomez-Cadenas (2013) demonstrated that a transient increase in jasmonic acid is required for synthesis of ABA in roots. In their experiment, jasmonic acid levels in citrumello roots experience a spike (8 times higher than control) prior to increasing levels of ABA in response to decreased soil water potential.

In *A. thaliana*, JA-Ile interacts with Jasmonate Zim (JAZ) transcription repressor complexes (Pauwels, et al., 2010; Fernandez-Calvo, Chini, Fernandez-Barbero, Chico, & Gimenez-Ibanez, 2011; Niu, Figueroa, & Browse, 2011) to effect the expression of Ethylene Response Factor (ERF) genes (which require ethylene for activation) and myelocytomatosis (MYC) genes. ERF genes are involved in defense against necrotrophic pathogens (pathogens that actively kill infected tissue) (Berrocal-Lobo, Molina, & R., 2002; Lorenzo, Piqueras, Sánchez-Serrano, & Solano, 2003). MYC genes are involved in defense against herbivorous insects and certain pathogens as evidenced by the increased resistance to *Phytophthora* spp. and *S. sclerotiorum* (Kazan & Manners, 2012; Lorenzo, Chico, Sanchez-Serrano, & Solano, 2004). MYC genes lead to the production of antirepellants, antinutritive compounds, and toxins (Pieterse, Does, Zamioudis, Leon-Reyes, & Wees, 2012; Howe & Jander, 2008).

Salicylic Acid in water stress and disease defense

Salicylic acid (SA) is a phenolic compound that induces pathogenicity-related gene expression by targeting the Nonexpressor of PR Genes1 (NPR1) polymer monomerization via changes in redox state. NPR1 monomers interact with transcription factors of pathogenicity-related-genes in *Arabidopsis thaliana* (Pieterse, Does, Zamioudis, Leon-Reyes, & Wees, 2012; Tada, Spoel, Pajerowska-Mukhtar, Mou, Song, & al., 2008). Salicylic acid induced defense genes act mainly against biotrophic pathogens that do not kill cells that they infect. SA is involved in systemic acquired resistance (Pieterse, Does, Zamioudis, Leon-Reyes, & Wees, 2012). It has also been shown to increase in response to drought stress (Munné-Bosch & Peñuelas, 2003), and it is a required signal molecule in drought stress pathways (Chini, Grant, Seki, Shinozaki, & Loake, 2004). Salicylic acid also interferes with ABA, disrupting water balance and stress response (Bostock, Pye, & Roubtsova, 2014), but SA can act also synergistically with ABA in guard cells to close stomata rapidly in response to pathogens that may enter the leaf through stomata (Vicente & Plasencia, 2011).

Role of Abscisic Acid in Disease Defense Signaling

In addition to regulating root growth and stomatal closure in response to drying soil, abscisic acid has been found to interfere with signaling responses to disease, both negatively and positively. ABA suppresses the SA pathway both upstream and downstream of SA synthesis (Cao, Yoshioka, & Desveaux, 2011; De Torres-Zabala et al., 2009; Jiang et al., 2010; Yasuda et al., 2008). Salicylic acid also interferes with abscisic acid (Bostock et al., 2014). The bacterial pathogen *Pseudomonas syringae,* that causes blossom blast, leaf lesions, twig die back, and cankers in woody perennials, utilizes antagonistic responses between ABA and SA to reduce the effect of SA-induced pathogenicity related defense genes (Bostock, Pye, & Roubtsova, 2014). Upon infection, *P. syringae* produces the protein AvrPtoB, which stimulates ABA production, in addition to a Jasmonyl- Isoleucine mimicking toxin called coronatine. These pathogenicity factors interact to suppress salicylic acid mediated defense genes, allowing *P. syringae* to successfully infect susceptible woody plants.

In *A. thaliana*, ABA has been demonstrated to act synergistically with JA induced MYC expression but antagonistically with ERF pathway (Abe, Urao, Ito, Seki, Shinozaki, & Yamaguchi-Shinozaki, 2003; Anderson J. P., Badruzsaufari, Schenk, Manners, & Desmond, 2004). This favors defense of insect herbivory over necrotophic pathogen infection in some cases, such as in the infection of *A. thaliana* by *Fusarium oxysporum* (Pieterse, Does, Zamioudis, Leon-Reyes, & Wees, 2012; Anderson J. P., et al., 2004). Jasmonic acid can also act synergistically on ABA signaling by encoding ABA receptor genes (Pieterse, et al., 2012; Lackman, et al., 2011).

However, not all necrotrophs react positively to increased ABA. Achuo, Prinsen, & Höfte (2006) found the necrotrophic fungus, *Botrytis cinerea*, was inhibited more in tomato plants exposed to drought stress that had elevated ABA levels. *A. thaliana* plants infected with *Phytophthora* spp. (Adie, et al., 2007) and *Sclerotinia sclerotiorum* (Perchepied, et al., 2010) were also shown to be resistant due to increased ABA levels and ABA/JA interactive signaling.

By imposing various levels of deficit irrigation on tobacco plants and maintaining those levels to allow for acclimation, (Ramegowda, et al., 2013) found tobacco plants previously exposed to moderate drought stress (especially 40%-60% of field capacity) had noticeably reduced cell death due to infection by both *S. sclerotiorum* and *P. syringae*, but severely stressed plants (20% FC) had similar extent of cell death to the control in *P. syringae* inoculated plants. Increased resistance under drought stress priming was associated with increased levels of ABA and levels of reactive oxygen species, i.e. O_2^- and H_2O_2. They also found that the defense genes PR-5 (pathogenesis-related protein-5) and PDF1.2 (plant defensin 1.2) increased in deficit irrigated tobacco plants. The latter of these genes is induced by the JA/ethylene pathway (Penninckx, et al., 1996), indicating that ABA does not always negatively affect the ERF branch of jasmonic acid signaling pathways. Jasmonic and salicylic acid pathways interact; however, they are often antagonistic towards each other (Pieterse, Does, Zamioudis, Leon-Reyes, & Wees, 2012), except when ethylene and jasmonate signals are induced prior to salicylic acid in *A. thaliana* (Leon-Reyes, et al., 2010).

Effect of other Phytohormones and Signaling molecules

Ethylene and related metabolites increase in drought stressed shoots due to 1-aminocy clopropane-1-carboxylic acid (ACC) signals from drying roots in citrus (Gómez-Cadenas, Tadeo, Talón, & Millo., 1996; Liu, Yu, Cui, Sun, & Sun, 2007)

(Salazar, Hernández, & Pino, 2015). Ethylene increases the effect of salicylic acid induced pathogenicity related genes (De Vos, Van Oosten, Van Poecke, Van Pelt, & Pozo, 2005; Lawton, Potter, Uknes, & Ryals, 1994), and it is essential for Systemic Acquired Resistance (SAR) induction in tobacco (Verberne, Hoekstra, Bol, & Linthorst, 2003), but the transcription factors activated by ethylene suppress SA biosynthesis genes, reducing the accumulation of SA (Chen et al. 2009). Ethylene also works synergistically with the ERF branch of the JA pathway, but it acts antagonistically with the MYC branch (Pieterse, et al., 2012; Anderson, et al., 2004; Lorenzo, et al., 2004; Lorenzo, et al., 2003; Pré, Atallah, et al., 2008)

Hydrogen peroxide (H_2O_2) and Nitric oxide (NO) are also involved in ABA induced stomatal closure (Lu, Su, Li, & Guo, 2009) and in systemic acquired resistance (Pieterse, Does, Zamioudis, Leon-Reyes, & Wees, 2012). NO activates antioxidants and is involved in salicylic acid signaling pathway as a covalent molecule that aids in NPR1 oligomerization (Lindermayr, Saalbach, & Durner, 2005). Perchepied, et al. (2010) demonstrated that NO is an important component of defense against *S. sclerotiorum* in *A. thaliana* since mutants deficient in NO production were very susceptible to the disease.

In spite of the complicated nature of biotic and abiotic stress and the effect of water availability on disease development, there is decisive evidence that acclimating plants to drought stress can prime them to better defend against some pathogens as was evident with *S. sclerotiorum*, *P. syringae*, *O. neolycopersici* and *B. cinerea* as discussed earlier.

Water Stress effects on Viruses

Under drought stress conditions, viruses can be among the most problematic pathogens. Virus incidence can increase under drought conditions because some insect vectors tend to move off of native vegetation onto irrigated crops (Oswald & Houston, 1953). However, upon infection virus relations with drought stressed hosts are complicated and depend on the virus's biology and defense suppression mechanisms. As an example, abscisic acid has been found to be an important hormone in defense against certain viruses. For tobacco mosaic virus (Fraser & Whenham, 1989) and tobacco necrosis virus (Whenham, Fraser, Brown, & Payne, 1986) ABA has been shown to increase callus deposits and prevent systemic spread of virus particles.

In Bamboo Mosaic Virus, (Alazem, Lin, & Lin, 2014) demonstrated that tobacco and *A. thaliana* mutants deficient in ABA biosynthesis downstream of ABA 2 gene and exogenous application of both ABA and a chemical that reduces enzymatic activities involved in ABA synthesis decreased resistance to the virus compared with the wild type. In contrast to this, cucumber mosaic virus suppresses signaling in salicylic acid (Ji & Ding, 2001; Lewsey, et al., 2010), jasmonic acid (Lewsey, et al., 2010), and abscisic acid pathways (Westwood, et al., 2013). This confers drought tolerance in *A. thaliana*, but this is hypothesized to be more advantageous to the virus than plant hosts.

Diseases that arise from over-irrigation.

It is beneficial to discuss issues that arise from over-irrigation because water supplies are not always limiting in semi-arid regions. Water policy may dictate that water supplies be increased, even in if only temporarily, when drought conditions subside. Under such conditions, it is often the temptation to over-irrigate, especially under conditions of high evapotranspiration. Over-irrigation can also be a problem in irrigation systems that distribute water in high volumes, e.g. furrow or flood irrigation, or unevenly, where water can puddle or be above field capacity more frequently than the other areas of the field, such as in near surface drip irrigation of potatoes near emitters (Browne, DeTar, Sanden, & Phene, 2002). For instance, Browne et al. (2002) found a higher incidence of the stem rot in potato caused by *Sclerotinia rolfsii* in sprinkler irrigated and near surface drip irrigated vines compared to sub-surface irrigated drip irrigation.

Flooded soil can negatively affect crop growth by reducing the diffusion of oxygen to plant roots and increasing CO_2 levels, causing reduced transpiration and root damage (Jackson, 2002). Plants respond similarly to waterlogged soils as they do to drying soil. They increase hormonal root to shoot signaling leading to stomatal closure. Also, increased ethylene in foliage can cause epinasty symptoms in severe cases (Jackson, 2002). A number of soil pathogens thrive in moist soil, including *Sclerotinia sclerotinium* (Heffer Link & Johnson, 2012) and other *Sclerotinia* spp., *Rhizoctonia solani* (Tsror, 2010; Muriungi, Mutitu, & Muthomi, 2014), and pathogens in the class Oomycota. Soil borne pathogens in the class Oomycota, commonly known as water molds and including mainly *Phytophthora* and *Pythium* species, are heavily favored by moist soil. One particular stage in the life cycle depends on free soil water to migrate toward plant roots. *Phytophthora* *capsici* can infect roots in waterlogged soils within 24-48 hours (Palloix, Daubeze, & Pochard, 1988).

Over irrigation can also have a negative effect on foliar, stem, and fruit disease symptoms as well, even if plants are not watered above canopy. For example, in a study of 110 orchards in Spain (Vicent, Botella-Rocamora, López-Quílez, de la Roca, Bascón, & García-Jiménez, 2012) found a strong correlation between soil waterlogging in citrus orchards and prevalence of citrus canker and brown fruit rot caused by *P. citrophthora*. They suggested increasing soil drainage, especially in low-lying areas, along with avoiding other traditional practices like scoring branches to improve fruit quality. Even though drought stress has also been associated with *Phytophthora* diseases in previous studies of various crops (Erwin & Ribeiro, 1996; Vicent, Botella-Rocamora, López-Quílez, de la Roca, Bascón, & García-Jiménez, 2012), Erwin and Ribeiro (1996) found no significant link with deficit irrigation. However, it should be noted that regulated deficit irrigation strategy was not defined in the paper. The question was posed to producers whether or not the practice is used.

Effect of Drought stress on Arthropod Pests

Drought stress affects arthropod pests differently depending on their feeding guild, ability to detoxify plant toxins, and ability to undermine other plant defenses. In a survey and meta-analysis of drought/insect herbivore interaction papers dating from 1955 to 2004, Huberty & Denno (2004) looked at the response of different feeding guilds to drought stress. The majority of studies on sap feeding insects showed a negative response to drought stress. Chewing insects were reported to respond equally positively and negatively to water stress. Phloem, mesophyll feeders, and gall formers with chewing mouthparts responded overwhelmingly negatively to drought stress in the reviewed studies. On the other hand, 50% of the studies reported a positive response of borers to drought stress, with increased survivorship on drought stressed trees. They found through meta-analysis of the papers surveyed sap feeders survivorship and density suffered on drought stressed plants, even though there was no difference in fecundity, oviposition, or relative growth rate. Of the sap feeders, mesophyll feeders had a stronger negative response to drought stress than phloem feeders. Chewing insects only had a lower rate of oviposition on drought stressed plants, consistent with the finding of equal positive/negative effect.

Plant physiological changes in response to drought stress determine the success of herbivorous arthropods. Reallocation of carbohydrate photosynthates during moderate drought stress causes plants that are not actively growing shoot tissues to put these resources into tissue maturation (Mattson & Haack, 1987). This has been shown to lead to thicker cell walls, more fiber and conducting elements, and secondary metabolites, including terpenes, alkaloids, and waxes (Mattson & Haack, 1987), that can aid in protection against phytophagous arthropods (Koul, Walia, & Dhaliwal, 2008) and diseases (Dixon, 2001). However, this differentiation diminishes with increasing stress (Mattson & Haack, 1987).

Sugars and sugar alcohols also increase during more severe drought stress, but complex carbohydrates decrease (Mattson & Haack, 1987; Kramer, 1983). Sugars and sugar alcohols compounds are known to be attractants and feeding stimulants to many phytophagous insects. Ethanol, an ethylene derivative, is considered an attractant to wood eating insects like cerambycids and scolytids (Dunn, Kimmerer, & Nordin, 1986; Haack & Slansky Jr., 1987). Evidence shows that some insect species, such as the spruce budworm (*Choristoneura fumiferana* Clem.) and migratory locust (*Locust migratoria* L.) have peak feeding at high concentrations of sucrose, usually found in water stressed hosts (Mattson & Haack, 1987).

Spider mites and other phytophagous mites are highly dependent on a controlled micro-environment with high humidity and temperature. The flat citrus mite or false spider mite, *Brevipalpus californicus* (Banks), is favored by well-irrigated citrus trees in hot weather that are believed to create a boundary layer and humid conditions in thick canopies (Childers & Rodrigues, 2011). It is suggested that trees be pruned to create a more open canopy and increase airflow to reduce inner canopy humidity. Partial root zone drying may positively affect control of the flat citrus mite by reducing vigor, allowing for a more open canopy, and reducing transpiration.

Spider mites, (*Tetranynchus* spp.), have a very large host range (Zhang, 2008), and they are favored by high temperatures and manage their microenvironment by producing webbing. Spider mites also tend to be more successful on drought stressed plants (Youngman & Barnes, 1986; Stavrinides, Daane, Lampinen, & Mills, 2010) as well as thoroughly watered plants but not moderately stressed plants (English-Loeb, 1990). Youngman & Barnes (1986) researched the interaction of water stress and spider mites in almond trees. They found that trees not irrigated for one month had significantly greater spider mite eggs, nymphs, and adults, especially toward the end of the experiment when numbers were 2-3 times greater. Populations of spider mites crashed shortly after this, and this drop was attributed to increases in predatory species. Mite infestations also significantly lowered stomatal and mesophyll conductance and photosynthesis on all but one sample day in the 1982 trial year and about half the sampling days in 1983.

Later research by English-Loeb (1990) on bush beans (*Phaseolus vulgaris*) demonstrated that, under several levels of drought stress, spider mite populations were lowest under moderate drought stress and worse in well-watered and severely stressed beans, especially in the presence of spider mite predators. Under the best of conditions, it is difficult to manage spider mite populations because of their high reproductive rate, making it important to manage water stress when faced with spider mite infestations under favorable climatic conditions.

Twig, stem, and trunk borers are more attracted to water stressed trees than well-hydrated trees. Most studies on drought stress and wood-boring insects are on forest trees, but a number of species of beetle and Lepidoptera larvae in the family Sessiidae attack fruit trees (Barrett, 2014). Cavitation, or the formation of air bubbles in xylem canals, produces audible to ultrasonic noises that can attract many bark and trunk boring insects, such as those in the families Buprestidae and Cerambycidae (Barr, 1969; Carlson & Knight., 1969; Mattson & Haack, 1987). Based on evidence from a number of studies, White, (2015) argued that the cambium of drought stressed trees becomes highly enriched due to reallocation of nutrients from senescing tissue into storage. This may contribute to improved survival and development of phloem feeding insects.

Severe drought stress also reduces the ability of many trees to produce sap necessary to pitch boring insects and prevents them from infesting the cambium layer (Mattson & Haack, 1987). Hanks & Paine (1999) studied Eucalyptus longhorned beetle (*Phoracantha semipunctata* Fab.) colonization on pot-grown *Eucalyptus* trees subjected to water stress. They found a negative linear relationship between larval gallery length and leaf water potential of the tree and between percent cambium destroyed and leaf water potential when only five larvae were transferred to the tree. However, when 50 larvae were transferred to a tree, a positive linear relationship was observed, indicating that under increased *P. semipunctata* pressure, there is greater success on non-stressed trees and drought stressed trees receive less damage. Hanks & Paine (1999) also found that kino (or gummosis) was produced only in trees with an average of -1.13 MPa (under moderate drought stress) while trees with an average of -2.27 MPa (severe water stress) did not produce kino. However the authors were not able to link kino production with decreased damage or infestation. However, they did find that larvae were increasingly less able to infest the cambium with increasing bark moisture indicating water content was important in defending against infestation.

Phloem feeding insects may perform better in drought stressed plants because phloem tends to be enriched in solutes, especially nitrogen. This would be especially important to insects, such as aphids, that must expend energy to concentrate it. Wearing & van Emden (1967) studied the effects of drought stress in bean (*Vicia faba* L.), marigold (*Calendula officionalis* L.), and Brussels sprouts (*Brassica oleracea gemmifera* Sulz.) on populations of various aphids and found mixed results. No significant differences were found in populations of *Aphis fabae* (Scopoli) however, greater numerical levels of *A. fabae* were found in water stressed marigolds. *Myzus persicae* (Sulzer) populations tended to be greater in mildly stressed plants and significantly lower in marigolds severely water stressed. *Brevicoryne brassicae* L. did show a negative linear relationship with increased drought stress. Wearing & van Emden (1967) suggest that these aphid species react differently to enriched phloem sap and reduced turgor pressure.

In a follow up study by Wearing (1967), fecundity of *M. persicae* and *B. brassicae* increased in young and mature leaves but generally decreased in older leaves with increasing drought stress. This may be because nitrogen compounds including amino acids (such as proline, a major constituent of osmotic potential adjustment), nitrates, and betaine increase in younger tissue and decrease in older tissues and roots under drought stress (Mattson & Haack, 1987).

Xylem sap feeding insects, such as leafhoppers or sharpshooters (Cicadellidae), are affected by the nutritional content of xylem sap, which is lower than phloem, as well as pressure tension of xylem sap. The glassy-winged sharp shooter (*Homalodisca vitripennis* (Germar): Hemiptera) is the vector for *Xyllela fastidiosa*, the causal agent of Pierce's disease in grape. *X. fastidiosa* also infects orange, almond, and oleander, where it affects water transport to the canopy. The sharpshooter is a xylem feeding insect with greater than 100 hosts (Hoddle, Triapitsyn, & Morgan., 2003; Redak, Purcell, Lopes, Blua, Mizell III, & Andersen., 2004). Krugner, et al. (2009) studied the effect of deficit irrigation on glassy-winged sharp shooter in sweet orange and found that populations were significantly lower in the 60% crop evapotranspiration (ET_c) treatment compared to 80% crop evapotranspiration. Trees watered at 100% crop evapotranspiration had intermediate population levels that tended to be similar to 80% in early summer and 60% in late summer. With few exceptions, trees facing moderate water stress (80%) supported the greatest number of glassy winged sharpshooter adults. They also found no decrease in effectiveness or number of predators and parasitoids in drought treatments. The authors indicated that glassy winged sharp shooters on trees with moderate water stress might benefit from concentrated xylem sap. Glassy-winged sharp shooters on severely stressed trees and well- watered trees may expend more energy extracting xylem sap under increasingly negative tension or concentrating dilute xylem sap, respectively, thus reducing their fecundity or preference.

Chewing insects, such as the lepidopteran larvae *Mamestra brassicae* L. have been shown to oviposit more on drought stressed cabbage plants (Weldegergis, Zhu, Poelman, & Dicke, 2015); however, they did not perform significantly better on drought stressed plants. Additionally, drought stress did not signal *Microplitis mediator* (Haliday), a common parasitoid of *M. brassicae*. Only volatiles released in response to herbivory attracted the *M. mediator*. Weldegergis, Zhu, Poelman, & Dicke (2015) found that ABA and JA levels were significantly higher in response to *M. brassicae* on cabbage. They found that salicylic acid levels were higher in drought stress plants independent of herbivory. In contrast, Noor-ul-Ane, Arif, Gogi, & Khan

(2015) found that populations of cotton bollworm (*Helicoverpa armigera* Hübner) larvae were significantly lower on drought resistant cotton varieties subjected to drought stress, but percent damage was higher on most varieties under drought stress than the well-watered control.

Serra et al. (2013) studied the effect of regulated deficit irrigation and partial root-zone drying on grapevines at 80% and 40% on populations of two leafhopper species in the subfamily Typhlocybinae, *Jacobiasca lybica* (Bergevin and Zanon) and *Zygina rhamni* (Ferrari) in Sardinia. These leafhoppers are piercing sucking insects that feed on mesophyll leaf tissue, causing speckling and reduced photosynthetic capacity. Grapes under partial root-zone drying at 40% had the largest yield and water use efficiency and supported the second lowest levels of *J. lybica*. The authors found no significant difference in levels of *Z. rhamni*, which is thought to not cause economic damage in vineyards in Italy. Daane & Williams (2003) studied the effect of manipulating irrigation on populations, growth, and preference of the leafhopper species *Erythroneura variabilis* (Beamer) on Thomson seedless grapevines across multiple generations. They watered the vines from 0% to 140% of lysimeter evapotranspiration in 20% increments and found that *E. variabilis* in caged plots performed worse with decreasing irrigation, except in the first generation of introduced leafhoppers. Daane & Williams (2003) found that nymphal size (dry mass) increased with irrigation level in the second and third generation. Also, the number of nymphs per leaf between generations increased, with the third generation showing a positive linear relationship between nymphs per leaf and irrigation level. There was also increased movement of adults from deficit-irrigated vines to fully- or over-irrigated vines. Adults per leaf were lower in deficit irrigation toward the end of the season, from late July to August. The authors were unable to prove increased nymphal mortality, but they showed that there was decreasing nymph density as the season progressed. Leafhopper densities were found to be correlated with shoot length, leaf area, and water potential, indicating that the reduction in vigor also influenced *E. variabilis*. In a separate experiment on oviposition, they found that females oviposited 55% more on vines irrigated at 120% than at 60% crop evapotranspiration.

Costello (2008) found similar results in a study on the effects of regulated deficit irrigation on *Erythroneura elegantula* (Osborn) and *E. variabilis*, two important pests of grapevine in California. Costello imposed 25% and 50% CROP EVAPOTRANSPIRATION between berry set and veraison, berry ripening, and counted leafhopper nymphs weekly starting two to three weeks before deficit into August. He found consistently lower nymph levels in the second generation with reductions of 39-52% between the first and second generation. These reductions occurred near the end or immediately following the deficit period. The author argues this makes season long deficit irrigation unnecessary for controlling leafhopper. Costello (2008) hypothesized that this may be due to increased cuticle thickness of the leaves or lower leaf water potential making it more difficult for nymphs to feed. These results demonstrate that deficit irrigation can aid in the control of leafhopper populations in vineyards.

Even though there are mixed reactions of arthropod pests and plant pathogens to drought stress, it is clear that the water status of crops significantly affects the outcome of infection or infestation. With this in mind, monitoring irrigation is an essential first step to using irrigation water optimally and as an intrinsic part of an integrated pest management program. In many cases, avoiding plant stress is crucial to meeting these goals, but this is not simply achieved by just watering crops more to avoid drought stress. It is important to create the best environment for healthy plant growth, and this may often mean reducing irrigation when necessary to improve a crops tolerance to drought stress and/or pest pressure.

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Appendix A: Penman-Monteith Equation

Equation 2.1. Crop Evapotranspiration

$$ET_o = \frac{0.408\Delta(R_n - G) + \gamma \frac{C_n}{T+273}(e_s - e_a)u_2}{\Delta + \gamma(1 + C_d u_2)}$$

- Delta represents the “the slope of the saturation vapor pressure at mean air temperature curve (kPa °C^{-1})
- Rn=net radiation flux, T is the temperature in degrees Celsius
- G= sensible heat flux into soil
- Gamma= Psychometric constant)
- E_s-e_a= vapor pressure deficit.
- U_2= wind speed
- C_n and C_d are reference crop specific coefficients