Plant Water Use and Growth in Response to Soil Salinity in Irrigated Agriculture

by

Benjamin Reade Kreps Runkle

A dissertation submitted in partial satisfaction of the requirements for the degree of Doctor of Philosophy in Engineering – Civil and Environmental Engineering in the Graduate Division of the University of California, Berkeley

Committee in Charge:
Professor John A. Dracup, Co-chair
Professor Xu Liang, Co-chair
Professor Dennis Baldocchi
Professor Garrison Sposito

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Plant Water Use and Growth in Response to
Soil Salinity in Irrigated Agriculture

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To RD

Who has taught me to sail in scale
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Abstract

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Soil salinity levels are an important determinant of plant evapotranspiration and carbon uptake. In this dissertation I develop, evaluate, and test a model of plant evapotranspiration and carbon uptake in the context of a saline soil environment, and drive the model using leaf physiological parameters determined from field measurements. This modeling work is performed in the context of three research questions: (1) How are leaf gas exchange parameters characterizing photosynthesis in perennial pepperweed best determined for seasonal scale landscape flux analysis? (2) How can the effects of soil salinity on root water uptake be represented in order to account for changes in the diurnal cycle and in the uptake of carbon dioxide by plants? (3) How sensitive are modeled results to changes in model input parameters, and how may these sensitivities limit the predictive abilities of the model? These questions are assessed using data from a relatively wet pasture-peatlands in the San Francisco Bay –Sacrament River Delta region of California, with the dominant land-cover species perennial pepperweed (*Lepidium latifolium*), a mildly salt-tolerant and invasive herbaceous weed.

Presented in this research is a characterization of pepperweed as a highly capable invasive species, able to take advantage of local resources such as light, carbon, water, and nitrogen. Modeling results from each section also demonstrate its ability to photosynthesize under higher temperatures and vapor pressure deficits than standard plant models suggest. Incorporating soil salinity into a whole-plant model increases the ability to describe how different soil and atmospheric parameters influence evapotranspiration and photosynthesis in such an environment. The model’s sensitivity analysis reveals two pairs of parameters that may constrain each other, and demonstrates how improved measurements of plant conductance and leaf water potential can constrain other portions of the parameter space.
Chapter 1: Plant Responses to Soil Salinity in Irrigated Agriculture

Understanding the interactions and relationships between the soil, plants, and the atmosphere at different temporal and spatial scales requires making assumptions about how the governing physical, chemical, and biological processes at one scale influence the governing processes at another scale. Better process-based understanding across and between scales allows for a host of scientific and engineering questions to be resolved. This dissertation examines how soil water and salinity conditions influence a plant’s leaf-based processes (water release, carbon uptake), and how a heterogeneous landscape of such plants influences field-scale gas fluxes. The research questions investigated have ecological, agricultural, and engineering implications that cross even more scales, and could involve processes influenced by physical phenomena ranging across scales that include pore-scale soil water dynamics, global climatic patterns, the effects of daily watering regimes on decadal landscape changes, and the implications of long-term changes in climate on future annual crop yields.

The study of the role soil salinity plays in plant processes is important: current Food and Agricultural Organization reports (FAO, 2005) indicate that over 800 million hectares, equivalent to 6% of the world’s total land area, are affected by saline or sodic soils. Of the current 230 million hectares of irrigated land, 19.5% suffer from excessive salinity. High salt levels in agricultural soil often derive from irrigation water that contains trace amounts of minerals; these minerals accumulate at the soil surface as the water evaporates (Rozema and Flowers, 2008). This process of salinization is nearly inevitable in irrigated systems in dry environments, and has led to widespread abandonment of farmland in arid regions. The infiltration of water through saline soils also enhances the mobilization of soil clay particles, which then swell, disperse in the soil solution, clog soil pores and reduce the pore diameter size. This progression increases the likelihood of waterlogged soils, which encourages even more soil degradation through weathering (Sparks, 2003). Poor drainage can further compound soil salinization by increasing the depletion rates of soils and other parent materials, which further promotes the soil salt content. All of these processes can at certain levels impair plant growth and crop yield by increasing toxic and osmotic stresses, and have important implications for agricultural water use. Moreover, several authors warn that problems associated with soil salinization will worsen as a result of expected climate change (Schofield and Kirkby, 2003; Yeo, 1999). They write that under climate change there may be increased land-ocean interactions in coastal areas and increased irrigation needs from higher evaporation rates in inland areas.

The effects of salinization can be studied at many spatial and temporal scales, and the relationships between patterns that develop at one scale and the underlying processes at another scale tend to be understudied. Representative scales of interest are shown in Figure 1-1. Spatially, salinization can be examined from the root zone to the landscape, and temporal scales of importance range from the quick response of plants to changing light conditions or the influence of solute concentrations on seasonal to interannual changes in agricultural yield.
Figure 1-1: Representative temporal and spatial scales where salinization processes are of interest.

Current models relating soil salinity to plant transpiration and carbon uptake often ignore important leaf-level processes governing these fluxes. Soil salinity changes the effective soil moisture availability through its creation of an osmotic gradient between root and soil, and these effects change the movement of water from root to leaf. Salinity-induced reductions to leaf water potential can force it across critical thresholds where wilting and cavitation severely influence carbon uptake. Leaf-level biochemistry depends on the concentration of carbon dioxide at the site of photosynthesis, which depends on the stomatal aperture, which is often governed by water availability for transpiration. The feedbacks that develop between these processes suggest that root water status and rates of photosynthesis are intricately related. Season-averaged metrics of water use efficiency often do not apply at smaller time-scales, and leaf-average characteristics do not always apply at the field scale. The interactions between these behaviors at different scales are studied in this dissertation through a combination of numerical modeling and measurements at the leaf and field scales.

1.1 The research questions

I plan to address the following three questions:

1. How do leaf gas exchange parameters characterize the response of an invasive species to soil salinity?
2. How does soil salinity change diurnal transpiration and uptake of carbon dioxide in plants?
3. How sensitive are modeled results to changes in model input parameters and to field data collected to drive the model?

These questions are asked in the setting of a relatively wet pasture-peatlands managed ecosystem in the San Francisco Bay/Sacramento River Delta region of California. The dominant land-cover...
species is perennial pepperweed (*Lepidium latifolium*), a mildly salt-tolerant and invasive herbaceous weed.

This dissertation will be presented by building and then testing a model where physical processes at smaller, leaf-level scales are aggregated to the plant-scale and then compared to field-level measurements. This model will be tested and analyzed numerically for its ability to replicate and predict field-scale behavior. A sensitivity analysis will determine the range of conditions under which the model’s results will be valid. Conclusions drawn from this range of conditions allow the model to be relevant beyond the field settings under which it was developed. The models will uncover important physical relations, from interactions of plants with the atmosphere to interactions within the ground’s subsurface to, finally, field and landscape scale implications of high soil salinity levels. The combined results of these investigations will be useful for applications in land-surface modeling, water resources planning, and agronomic decision-making, and will help increase the efficiency of water use and raise crop yields.

1.2 Leaf-scale photosynthesis parameterization

The leaf’s biochemical properties govern much of the short-term response of a plant to its environment: how open or closed are the stomata?; how much water is transpired to the atmosphere?; how much carbon is assimilated by photosynthesis or released in respiratory processes? Models of these processes have been well-established (Farquhar et al., 1980) but require parameterization with species-specific properties, often measurable in the field. This dissertation publishes for the first time the governing leaf-level parameters of perennial pepperweed, *Lepidium latifolium*, a heavily invasive species of concern in the western United States for which knowledge of leaf physiology is missing. This new parameter set includes estimates of daytime respiration, maximum carboxylation efficiency, maximum electron transport rate, and stomatal conductance to CO$_2$ and H$_2$O transfer.

Determining this set of parameters required developing a measurement scheme to determine the parameters dominating processes at different conditions. Once the data collection was completed, deriving the parameters from measurements required additional numerical modeling, such as fitting physically-derived non-rectangular hyperbolae to the photosynthesis-light or photosynthesis-CO$_2$ curves. This section focuses primarily on resolving research question (1) above, by providing the set of instantaneous leaf gas exchange parameters that will be used to resolve seasonal or annual landscape fluxes.

1.3 Biometeorological soil-vegetation-atmosphere transfer modeling framework

Applying an existing biometeorological framework to model plant water relations in the presence of salinity, I will quantify and prioritize some of the nonlinear, feedback and feed-forward effects of increased soil osmotic pressure on stomatal conductance, transpiration, and plant carbon dioxide intake. A conceptual picture of this model is presented in Figure 1-2. Current models of plant water use and photosynthesis in saline soils tend to operate at the daily or seasonal time scale, and are often derived from empirically-derived threshold effects of salinity. The proposed model operates at a more frequent time-step (half-hourly), and represents the physical processes that allow saline soils to change plant processes.

In answering research question (2) above, this section will also explore the following two research sub-questions:
i. Which soil-plant-atmosphere relations best represent the effects of high salinity on plant behavior at the field scale?

ii. How does including the diurnal pattern of salinity’s effect on plant water use efficiency change estimates of plant growth and water use (relative to current models of salinity)?

Figure 1-2: The Osmotic SVAT model nests relationships at different spatial scales, from the leaf to the plant to the field. Terms and processes are defined in Chapter 3.

1.4 Validation with field data

By comparing models of leaf, plant, and field behavior to data collected in the field, the model can be locally validated, and field-specific management questions can be resolved. Leaf measurements of rates of photosynthesis and transpiration, pre-dawn and mid-day leaf water potential, and instantaneous stomatal conductance, can be compared to field level flux measurements of water vapor and carbon dioxide. Estimates of the field’s leaf area index are used to assist in moving between the leaf and field scales. Each set of measurements can be compared to the model’s output to determine where and how the model does or does not perform well.

The particular management questions that this model assists in answering include irrigation scheduling, land management (e.g., fallowing) and expected field responses to changing climate conditions. Using the model as a predictive tool to assess these questions will provide increased scientific certainty with which to evaluate different policy or management options.
1.5 Model sensitivity

The model’s sensitivity to input data uncertainties and parameter estimation errors can be determined through a sensitivity analysis known as the generalized likelihood uncertainty estimation (GLUE), which accounts for multiple sources of input errors that are processed nonlinearly through the overall modeling framework (Beven and Freer, 2001; Beven et al., 2008). This framework determines through a bootstrap-type approach the most important parameters to assess accurately. As such, it offers an opportunity to improve upon the model’s predictive power. The model’s sensitivity analysis reveals two pairs of parameters that may constrain each other, and demonstrates how improved measurements of plant conductance and leaf water potential can constrain other portions of the parameter space.

This section examines the questions of model sensitivity raised by research question (3), and also answers the following two research sub-questions:

i. How certain are we of model outputs, in particular for different climate change scenarios?
ii. What do model simulations reveal about plant responses to different soil salinity conditions?

1.6 Discussion

The dissertation will conclude with a discussion of its impact on understanding the water and carbon relations of our environment. The wider application of the model developed within should create better irrigation and land management decisions, based in the enhanced understanding of water use efficiency in saline environments. The model’s relative simplicity allows its application in comparatively data-poor regions, such as developing nations where the impact of salinity may be of relatively greater importance yet where remediation strategies may be less likely implemented.

Future applications of this modeling strategy include a wide set of interesting and important research questions. This physically-based salinity model can be “upscaled” to support landscape to regional analysis by providing some local context for remotely sensed data or regional land surface model results. Its focus on salinity encourages its application to regions where seawater intrusion into the groundwater is changing ecological productivity. Finally, the model’s development has expanded the ecohydrological framework used to evaluate the interactions between plant communities and the hydrological cycle, so could be applied to a large set of ecological and hydrological analyses.
1.7 Works cited
Yeo, A., 1999. Predicting the interaction between the effects of salinity and climate change on crop plants. Scientia Horticulturae, 78(1-4): 159-174.
Chapter 2: Leaf physiology of a perennial herb, Sherman Island, CA

2.1 Introduction
Modeling plant photosynthesis in environmental conditions is complex and requires aggregating interactions between different cells and organelles in different light, CO₂, and temperature environments (von Caemmerer, 2000). Mechanistic models of photosynthesis commonly derive from the work of Farquhar et al. (1980), who investigate the steady-state gas exchange of leaves in their response to light, CO₂, O₂, and temperature. Parameterizing this model requires species-specific measurement strategies, as the governing parameters change over one to two orders of magnitude across species (Wullschleger, 1993), particularly at temperatures greater than 30°C (Leuning, 2002). This chapter examines the parameters governing leaf gas exchange in perennial pepperweed (*Lepidium latifolium*), the dominant, and invasive, land-cover species found growing on a flux-measurement site on California’s Sacramento-San Joaquin River Delta region (Sherman Island). These parameters will later be used to model field-scale plant behavior to predict how this landscape will respond to changes in environmental and climate conditions.

Investigating gas exchange processes on weeds is important for many reasons. These processes control plant water use, govern the comparative effectiveness of weeds and crops for using environmental resources, and determine the rate of carbon assimilation through the plant – a critical process for pesticide efficiency as well as the overall plant growth rate (Holt, 1991). The gas exchange models provide a base from which to predict weed responses to changes in CO₂ concentration, temperature, water levels and salt stress, and so should encourage land and water managers to analyze how future change scenarios may encourage or discourage the spread of unwanted species.

This chapter proceeds in the following manner. First, a review of current knowledge on *Lepidium latifolium* is presented, with a focus on its physiological characteristics. Then a short review of current leaf gas exchange modeling strategies is presented, and the modeling and measurement techniques used to derive key parameters of interest are explained. These key parameters include not just the limiting terms in allowing photosynthesis, but also consist of the terms more likely influenced by soil drought or salinity stress (such as internal and stomatal conductance). The work of a growing season’s field survey is introduced. Once the field data collection results and parameter modeling studies are shown, the key parameters and their uncertainties are summarized in a table. These parameters will finally be put into a comparative context to other species in the discussion section.

The key findings of the research presented in this chapter are:

1) High leaf nitrogen levels are found (2-6% nitrogen by dry leaf mass), particularly at the start of the growing season. The importance of nitrogen in determining the fitness of the plant and in the investment towards photosynthetic machinery has been reviewed previously (Franklin, 2007; Hikosaka, 2004; Hikosaka and Osone, 2009; Kergoat et al., 2008), but is of special interest for this invasive species.

2) The gas exchange parameters governing leaf response to incremental increases in carbon dioxide concentrations (C_l) and light (PAR) are derived from field survey measurements, and temperature-normalized to 25°C. The maximum rate of carboxylation $V_{c,max}$ averages 125±25 μmol m⁻² s⁻¹ (n=43); the maximum electron transport rate $J_{max}$ averages 222±37 μmol m⁻² s⁻¹ (n=43); and the daytime respiration rate $R_d$, averages 2.38±1.38 μmol m⁻² s⁻¹ (n=57). While it is difficult to discover underlying functional dependencies that drive variation in parameters, it
is clear that these parameters are indicative of a highly capable weedy herbaceous species.

3) The internal conductance to CO\textsubscript{2}, \( g_i \), is deemed infinite in most cases (all A-C\textsubscript{i} curves, the Laisk method, two-thirds of the constant-J method data), or hard to characterize under other methods (in particular, the variable-J method). When finite estimates of \( g_i \) are derived from the data there are numerical or optimization issues that prevent a decisive conclusion regarding internal cellular resistances. Tests in non-photorespiratory conditions show that the suitability of the variable-J method is limited to non-saturating light exposure.

4) An attempted new, non-rectangular hyperbola fitting method to generate better estimates of the photo-compensation point \( I^* \) than the traditional Laisk method, finds numerical uncertainties equal to measurement uncertainties. Reverting to the traditional method of forcing an intercept between three to four linearized segments of low-light A-C\textsubscript{i} curves uncovers an average value of \( I^* \) equal to 4.35 Pa (±1.21 Pa, n=6).

5) The Leuning (1995) model of stomatal conductance to water vapor provides an adequate \( r^2 = 0.765 \) prediction of leaf response to environmental inputs, given a slope term of \( a_1 \) equal to 18. The model does however underestimate stomatal conductance in low VPD conditions, where \( r^2 = 0.578 \) and other factors influence stomatal conductance.

2.2 Review of Current Literature

2.2.1 Review of L. latifolium

*Lepidium latifolium*, or perennial pepperweed, is an invasive species of concern throughout much of the western United States (Young et al., 1995), with special attention given to its spread in California’s San Francisco Bay-Sacramento River Delta region (Andrew and Ustin, 2006). Since its introduction to California in the 1930s, perennial pepperweed has rapidly and aggressively expanded its range through clonal root spreading and prolific seed production. It creates dense thickets of semi-woody stems that can reach up to 2 m in height, crowding out other species. Consequently, it threatens core ecological functions of riparian areas and hay meadows and disrupts agronomic fields through its spread in irrigation canals (Wilson et al., 2008; Young et al., 1998). While complete control of pepperweed is difficult, some success has been made through repeated application of chemical pesticide in combination with planting of native grasses and mechanical methods such as burning, mowing or disking (Renz and DiTomaso, 2006; Wilson et al., 2008).

The physiology of pepperweed has been studied in various ways in recent years. As reviewed in Francis and Warwick (2007), perennial pepperweed is an herb growing from rarely branched stout rhizomes or rootstocks, which are horizontal short thread-like roots. Its stem grows singly from the nodes of the rhizome and grows upright with many-branched upper stems. Its leaves grow in either basal rosettes or on the stems, with their size generally reduced with height on the plant. Occasionally the same root stock will send up multiple stems from the same base; this root stock will also generate basal rosettes before or after the stem’s growth is complete.

While tolerant to both drought and saturated soil conditions, pepperweed has been shown to grow best in lightly-watered soil conditions. Studies on the effect of root-zone saturation have shown that accumulated biomass is greatest when grown at soil matric pressures of -20 kPa and
decrease as soils become drier (e.g., biomass at -400 kPa was found to be less than 15% of the biomass in -20 kPa soils, with leaves wilting every day in the drier case). Pepperweed grew poorly, but survived, saturated soil conditions (Blank et al., 2002). Another study found that the mid-day photosynthesis of flooded plants was about 60-70% of the rate of unflooded controls (Chen et al., 2005), which, while reduced, was still amply adequate to ensure survival of the plants (Chen et al., 2002). The invasion of pepperweed to a field can also significantly alter soil chemical properties, nutrient cycling, and nutrient fluxes (Blank and Young, 2002).

The gas exchange processes of pepperweed have been studied to some degree, though to my knowledge the governing parameters for applying a process-based model (Farquhar et al., 1980) have not been reported. CO$_2$ enrichment studies (Blank and Derner, 2004) have suggested that CO$_2$ enrichment [699 µmol mol$^{-1}$ relative to 360 µmol mol$^{-1}$] may enhance the competitiveness of pepperweed relative to other plants. The enhanced CO$_2$ significantly increased the available pool of soil N in high fertility soil and increased the bicarbonate pool of extractable phosphorous. Higher CO$_2$ also allowed greater accumulation of plant biomass per unit of nutrient (i.e., nutrient use efficiency); though there is uncertainty whether further increases in CO$_2$ will see similar increases in resource use efficiency.

### 2.2.2 Review of photosynthesis model

Leaf-level net photosynthesis is widely modeled as the minimum of three rate-limiting processes: the RuBP-saturated rate of maximum Rubisco activity ($w_c$), the RuBP-limited CO$_2$ assimilation rate ($w_j$), often occurring under high intercellular CO$_2$ concentrations, and export-limited assimilation ($w_p$), with the relatively slower rate of production of triose-phosphates used to synthesize starch and sucrose, often occurring under very high CO$_2$ concentrations. This model is derived in Farquhar et al. (1980), and expanded upon and explained throughout the literature of the last thirty years (Harley and Sharkey, 1991; Sharkey, 1985; Sharkey et al., 2007; von Caemmerer, 2000; Yin et al., 2009).

The actual rate of carboxylation ($v_c$) at Rubisco’s location in the leaf is set by the minimum of the three potential rates (Farquhar et al., 1980; von Caemmerer, 2000):

\[
v_c = \min\{w_c, w_j, w_p\}
\]  

[1]

Based on the sequential diffusion of CO$_2$ from its concentration in ambient air ($C_a$), to the substomatal cavity ($C_i$), to the chloroplasts ($C_c$), the rate of photosynthesis (or assimilation, $A$) can be derived with an Ohm’s Law formulation:

\[
A = g_s(C_a - C_i) = g_m(C_i - C_c)
\]  

[2]

Where $g_s$ and $g_i$ represent the conductance of CO$_2$ through the stomata and internal cellular structure, respectively. Internal conductance is often called mesophyll conductance, and is then given the abbreviation $g_m$.

The Farquhar et al. (1980) model of photosynthesis describes the competition between CO$_2$ and O$_2$ for the Rubisco binding site in the processes of carboxylation and oxygenation, respectively. To account for these interactions and competitive inhibition, net assimilation $A_n$ is described by the difference between the assimilation rate and the CO$_2$ released in respiration:

\[
A_n = v_c - 0.5v_o - R_d = v_c\left(1 - \frac{\Gamma^*}{C}\right) - R_d
\]  

[3]

Here, $R_d$ refers to daytime respiration, and the term $(1-\Gamma^*/C)$ accounts for the proportion of recently assimilated carbon released in photorespiration. The term $C$ is left deliberately
ambiguous, as it was common in the past to use $C_i$ for this calculation, but with the increasing focus on internal conductance, $C_e$ is preferred if an adequate estimate of $g_i$ is possible. Physically, $C$ should represent the site of photosynthesis, which is in the chloroplast, so $C_e$ is the favored concentration value to use. As in Long and Bernacchi (2003), the photosynthetic compensation point ($\Gamma^*$) is the concentration of CO$_2$ where the photorespiratory efflux of CO$_2$ is equal to rate of photosynthetic CO$_2$ uptake (so $v_c=2v_o$). It is distinct from $\Gamma$, the CO$_2$ compensation point at which $v_c=2v_o+R_d$. The photosynthetic compensation point $\Gamma^*$ is defined:

$$\Gamma^* = \frac{0.5\Theta}{\tau}$$

Where the Rubisco specificity factor $\tau$, is derived from Rubisco kinetics as

$$\tau = \frac{V_{c,\text{max}}K_o}{V_{o,\text{max}}K_c}$$

And represents the relative influence between CO$_2$ and O$_2$ on Rubisco, where $K_o$ and $K_c$ are the Michaelis-Menten parameters for oxygenase and carboxylase, respectively, and $V_{o,\text{max}}$ and $V_{c,\text{max}}$, are the maximal rates of carboxylation and oxygenation, respectively. Substituting the actual rate of Rubisco activation into the photochemical description of photosynthesis gives

$$A = \min\{w_c, w_j, w_p\}\left(1 - \frac{\Gamma^*}{C}\right) - R_d$$

The individual carboxylation rates are as follows:

$$w_c = \frac{V_{c,\text{max}}C}{C + K_c \left(1 + \frac{O}{K_o}\right)}$$

$$w_j = \frac{J}{4(C + 2\Gamma^*)}$$

$$w_p = \frac{3V_{\text{tpu}}}{\left(1 - \frac{\Gamma^*}{C}\right)}$$

Where $w_c$, $w_j$, and $w_p$ are the potential rates of CO$_2$ assimilation that can be supported by Rubisco, RuBP-regeneration, and triose-phosphate utilization (TPU), respectively. At light saturation, $J$ is considered equal to $J_{\text{max}}$, but under lower light conditions, $J$ is estimated from the photon flux (Q) through a non-rectangular hyperbola (von Caemmerer, 2000):

$$J = \frac{Q_2 + J_{\text{max}} - \sqrt{(Q_2 + J_{\text{max}})^2 - 4\theta_{\text{PSII}}Q_2 J_{\text{max}}}}{2\theta_{\text{PSII}}}$$

Where $\theta_{\text{PSII}}$ is a curvature factor, for which various values are assumed in the literature: 0.95 is occasionally assumed (Daly et al., 2004; Leuning, 1990; 1995) though seems more appropriate to conifers (Ögren and Evans, 1993); von Caemmerer (2000) gives 0.7 as a good average value and Medlyn et al. (2002) suggest 0.9 but note that the parameter has only a slight effect on the estimated value of $J_{\text{max}}$. The value of 0.7 derives from studies on pea and spinach (Evans, 1987b; Evans and Terashima, 1987) where it was independent of growth irradiance and leaf chlorophyll content at saturating levels of CO$_2$. Setting $\theta_{\text{PSII}}$ to 0.7 seems reasonable for pepperweed since it is similar to spinach as an herbaceous species. Physically, the curvature factor takes a value of 1
in a slope-threshold type of limiting factor response, and a curvature of 0 indicates a rectangular hyperbola. \( Q_2 \) is the incident quanta used in electron transport through photosystem II (PSII):

\[
Q_2 = Q \alpha I (1 - f) \beta
\]  

[11]

Where \( \alpha \) is the leaf absorptance and \( \beta \) is the fraction of absorbed light that reaches photosystem II, and is assumed to be 0.5. The \( f \) parameter corrects for the spectral quality of light, and is assumed to be 0.15 (Evans, 1987a). \( Q \) is the incident irradiance.

The response of the entire photosynthetic system to temperature is significant, and varies with respect to genotype and environmental conditions, and may acclimate given different growth temperatures (Bunce, 2000; Bunce, 2008; Campbell et al., 2007; Medlyn et al., 2002). The temperature dependence of many of the parameters governing photosynthesis is commonly given by one of two forms of the Arrhenius function:

\[
f(T_k) = \exp\left(c - H_a \frac{T_k}{RT_k}\right) = k_{25} \exp\left(\frac{H_a(T_k - 298.15)}{298.15 RT_k}\right)
\]  

[12]

Where \( c \) is a scaling parameter, \( H_a \) is an activation term, \( k_{25} \) is the estimate of the parameter at 25°C, \( T_k \) is the leaf temperature in Kelvin, \( R \) is the ideal gas constant, and \( f \) yields the value of the parameter at the given temperature. If deactivation of the operating enzyme occurs at higher than optimal temperatures, one of two (equivalent) peaked functions is used:

\[
f(T_k) = \frac{\exp\left(c - H_a \frac{T_k}{RT}\right)}{1 + \exp\left(\frac{\Delta S \cdot T - H_d}{RT}\right)} = f(T_{opt}) \frac{H_d \exp\left(\frac{H_a(T_k - T_{opt})}{T_k R T_{opt}}\right)}{H_d - H_a \left(1 - \exp\left(\frac{H_a(T_k - T_{opt})}{T_k R T_{opt}}\right)\right)} \]  

[13]

Where \( H_d \) is the deactivation energy, \( \Delta S \) is an entropy factor, \( T_{opt} \) is the optimal temperature, \( f(T_{opt}) \) is the parameter value at the optimal temperature, and the other terms are defined following equation [12]. The second versions of these equations have clearer physical interpretations due to their inclusion of values at set temperatures, so are preferred here, though both are used throughout the literature.

The set of parameters governing these relationships has been compiled in several places (Bernacchi et al., 2003; Bernacchi et al., 2001; Medlyn et al., 2002). It is common in the leaf gas exchange literature to assume that \( K_c \) and \( K_o \) have similar values and temperature-response curves no matter the leaf; they are intrinsic to the photosynthetic machinery. The photosynthesis or photosynthesis compensation point \( I^* \) is often modeled as conserved across species, as is its response to temperature. Additionally, while the values of the other parameters may change, they should have similar activation and de-activation energies. While in many instances the temperature-response parameters of perennial pepperweed are estimated from field data, the state-of-the-science parameters used in Sharkey et al. (2007) provide both a useful starting point and a point of comparison (Table 2-1).
Table 2-1: Parameters governing temperature response of key Rubisco enzyme kinetic parameters for analysis of A-C\textsubscript{i} curves, taken directly from Sharkey et al. (2007), who cite several previous studies (Bernacchi et al., 2003; Bernacchi et al., 2002; Bernacchi et al., 2001; Harley et al., 1992b). Activation terms $H_a$ and $H_d$ have units [kJ mol\(^{-1}\)], $\Delta S$ has units [kJ K\(^{-1}\) mol\(^{-1}\)], the scaling factor $c$ is unitless, and the terms for $V_{c,max}$, $J$, $TPU$, $R_d$, and $g_i$ should be scaled by their value at 25°C.

<table>
<thead>
<tr>
<th>Parameters used for fitting</th>
<th>25 °C</th>
<th>$c$</th>
<th>$H_a$</th>
<th>$H_d$</th>
<th>$\Delta S$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K_c$ (Pa)</td>
<td>27.238</td>
<td>35.9774</td>
<td>80.99</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$K_o$ (kPa)</td>
<td>16.582</td>
<td>12.3772</td>
<td>23.72</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$I^*$ (Pa)</td>
<td>3.743</td>
<td>11.187</td>
<td>24.46</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameters used for normalizing</th>
<th>25 °C</th>
<th>$c$</th>
<th>$H_a$</th>
<th>$H_d$</th>
<th>$\Delta S$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$V_{c,max}$</td>
<td>1</td>
<td>26.355</td>
<td>65.33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$J$</td>
<td>1</td>
<td>17.71</td>
<td>43.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$TPU$</td>
<td>1</td>
<td>21.46</td>
<td>53.1</td>
<td>201.8</td>
<td>0.65</td>
</tr>
<tr>
<td>$R_d$ ((\mu\text{mol m}^{-2}\text{s}^{-1}))</td>
<td>1</td>
<td>18.7145</td>
<td>46.39</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$g_i$ ((\mu\text{mol m}^{-2}\text{s}^{-1}\text{Pa}^{-1}))</td>
<td>1</td>
<td>20.01</td>
<td>49.6</td>
<td>437.4</td>
<td>1.4</td>
</tr>
</tbody>
</table>

### 2.3 Methods to determine leaf physiology

#### 2.3.1 Modeling methods to determine photosynthesis parameters

Each of the crucial parameters for the model described above requires some modeling of field measurements; in each of these individual modeling efforts there are a range of uncertainties. Where possible, multiple methods of generating the same parameter are used and compared in order to reduce their uncertainty. The desire for independent assessments of these parameters drives much of the work described below.

The following section describes these modeling routines, and is organized as follows. Daytime respiration is estimated by the “Kok method” of analyzing changes in photosynthesis at low light levels. The photorespiration point and daytime respiration are jointly estimated by the “Laisk method” of analyzing the intersection of responses to CO\textsubscript{2} at different low light levels. The plant’s response to CO\textsubscript{2} and light are determined through the use of A-C\textsubscript{i} curves and A-PAR (for photosynthetically active radiation) curves, respectively. Fluorescence-based measurements provide estimates of the electron transport rate, which is used in two methods to determine the internal conductance to CO\textsubscript{2}.

#### 2.3.1.1 Daytime respiration $R_d$ and the photo-respiration point $I^*$

Mitochondrial respiration in leaves is used by plants to generate ATP for sucrose synthesis, to aid in modifying through the respiratory electron transport chain the reduction-oxidation conditions of photosynthetic activity, and to create the organic precursors such as C skeletons derived from the tricarboxylic acid cycle necessary for amino acid synthesis in the light, and is summarized in Shapiro et al. (2004). Thus the cumulative demands for energy and C skeletons influence the degree of mitochondrial respiration in the light. While once non-photorespiratory CO\textsubscript{2} evolution in the light was thought to be equivalent to that released during dark respiration, additional research has shown that respiration is partially inhibited during the light. Respiration in the light can range from 25-100% of respiration that occurs in darkness, in part resulting from the photosynthetic re-fixation of CO\textsubscript{2} released from mitochondrial respiration (Loreto et al., 1999) and in part resulting from inhibition deriving from the products of photosynthesis. These and other mechanisms are reviewed in Shapiro et al. (2004).

Methods for determining dark respiration in the light have used CO\textsubscript{2} gas exchange methods. Villar et al. (1994) compare the Kok method of analyzing the response of net photosynthesis with the Laisk method of analyzing the intersection of responses to CO\textsubscript{2} at different low light levels, and with gas exchange methods.
photosynthesis \( A \) to light at low intensities to the Laisk method that analyzes net photosynthesis at low \( C_i \) values and varying light intensities. These authors find that rates of dark respiration in the light are lower than respiration in the darkness, and the latter estimated by the Laisk method were 52% higher than as estimated by the Kok method. This difference is caused by the lower ambient \( \mathrm{CO}_2 \) concentrations required by the Laisk approach, which the authors explain (though not definitively) through the inhibiting effect of \( \mathrm{CO}_2 \) on certain enzymes seen in other studies.

2.3.1.1.a The Kok method to determine daytime respiration

The Kok method, as described in Sharp et al. (1984), assumes that the response of net photosynthesis to light is linear at low levels of irradiation, but near the light compensation point there is a break in the linear response, increasing the slope of the light curve due to a decrease in \( A \). This change is interpreted as a result of increased respiration due to a progressive disappearance of light-induced inhibition of dark respiration, and is called the “Kok effect”. Not accounting for this effect while fitting a line to the low light region of an \( A \)-PAR curve can generate a too-low apparent respiration. The method can therefore be corrected (Kirschbaum and Farquhar, 1987) so that the final estimate of \( R_d \) allows a linear regression of the quantum yield of RuP\(_2\) regeneration, \( V_j \), on absorbed light to pass through the origin, according to the relationship (combining equations [6] and [8]):

\[
V_j = \frac{(A + R_d) \left( 1 + \frac{2I^*}{C_i} \right)}{1 - \frac{I^*}{C_i}}
\]  \[\text{[14]}\]

This equation is applied to the \( C_i \) values taken in the A-PAR curve, for the \( C_i \) values within the range of measurements where Kok effects are not considered (e.g., at PAR > 50 ppm). The results of this method are tested for their sensitivity to estimates of \( I^* \), by comparing results when \( I^* \) at 25 °C is assumed to be 25 or 45 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). The results of this method are further compared to estimates derived from the slope of the fit to the initial section of the A-PAR curve.

The Kok effect is analyzed by investigating three curves with a high number of low PAR values. The transition PAR value separates the steep, low-light influenced region (where the ‘Kok effect’ dominates), and the region where the initial slope can be extended back to the \( y \)-axis to determine \( R_d \). It can be determined by incrementing the transitional PAR to find the point which minimizes the combined root-mean-square-error of two lines fit to data points on either side of that point.

2.3.1.1.b The Laisk Method to determine \( I^* \) and \( R_d \)

The parameters \( I^* \) and \( R_d \) can be derived using the Laisk method, as reviewed in Villar et al. (1994) and von Caemmerer (2000). \( \mathrm{CO}_2 \) response curves are taken at four different low irradiances, and the intersection of these curves in the low-\( \mathrm{CO}_2 \) range appears at \( C = I^* \) and \( A = -R_d \) (where there is neither enough light nor \( \mathrm{CO}_2 \) for photosynthesis to overcome photorespiration). These curves are fit in several ways to determine the sensitivity of the \( I^* \) and \( R_d \) estimates to the curve-fitting method:

1. **Individual linear fit**: Most traditionally, lines are fit to points where \( C_i \) is less than 100 ppm, in each light level. The intersection of these lines is estimated by inspection.
2. **Optimal linear fit**: Linear fits for points where \( C_i < 100 \) ppm are forced to share an intersect at the \((I^*, R_d)\) point that minimizes the root-mean-square error across all curves in each dataset.

3. **Non-Rectangular Hyperbola fit**: Fit all data taken in each curve to a non-rectangular hyperbola model; find the curve intersection by inspection.

4. **Optimal Non-Rectangular Hyperbola fit**: The non-rectangular hyperbolae are forced to intersect at the \((I^*, R_d)\) point that minimizes the root-mean-square error across all curves in each dataset.

Because of relatively flat optimization cost functions for the methods that force an intersect at \((I^*, R_d)\), some additional investigation and supervision is needed to discover the optimal, and physically plausible, solution. For instance, Method 4 uses as initial parameter estimates for its non-rectangular hyperbolae the parameters estimated in Method 3. The methods described above are also re-fit to determine whether the fit improves by using chloroplast CO\(_2\) concentrations \( (C_i)\) by changing \( g_i \). The “best” method and final parameter estimates are determined by comparing the results of these four fitting methods.

### 2.3.1.2 Light Response Curve Analysis

The light curve model estimates key parameters using a non-rectangular hyperbola fit to the full A-PAR curve following Marshall and Biscoe (1980a; 1980b) and Thornley and Johnson (1990). The model as derived by Marshall and Biscoe (1980a) assumes that net photosynthesis \( A_n \) (the net exchange of CO\(_2\) by an illuminated leaf) is equal to the difference between gross photosynthesis \( P \) and dark respiration \( R_d \) (the net photosynthesis at zero irradiance):

\[
A_n = P - R_d \tag{15}
\]

The rate of gross photosynthesis is derived as a non-rectangular hyperbola, and is given as:

\[
A_n + R_d = \frac{\phi I(A_{\text{max}} - \theta A_n)}{(1 - \theta)\phi I + (A_{\text{max}} - \theta A_n)} \tag{16}
\]

where \( I \) is the incoming irradiance, \( \theta \) is the ratio of physical to total resistance and \( \phi \) is the initial slope at zero irradiance, which is also known as the quantum yield of photosynthesis. The quantum yield is the rate at which a light-dependent process occurs relative to the rate of photon absorption by the system, and so indicates the efficiency with which absorbed light produces a particular effect. Quantum yield is the study of several reviews (Long et al., 1993; Skillman, 2008), and its measurement is widely taken and well-described (Long et al., 1996). Skillman finds a large variation in quantum yield with a median value of 0.06 mol CO\(_2\) mol\(^{-1}\) absorbed quanta, though admits that this value can change with the method used to derive quantum yield.

The curves were fit in two steps: first, by finding \( R_d \) and \( \phi \) by linear regression for all points with PAR between 45 and 205 \( \mu \)mol m\(^{-2}\)s\(^{-1}\). This initial step creates an estimate for \( R_d \), rather than \( R_{\text{dark}} \) since it is the daylight value of respiration since it removes the data-point influenced by the Kok effect. Second, these parameters were used to find the values of \( \theta \) and \( A_{\text{max}} \) which generated the best fit curve to the data (by minimizing the overall root-mean-square error of all points where PAR is greater than 45 \( \mu \)mol m\(^{-2}\)s\(^{-1}\)). The light compensation point (LCP) can also be derived; this value is the light level where net photosynthesis becomes positive.
2.3.1.3 A-C\textsubscript{i} curve Analysis

Datasets where the leaf is exposed to a variety of CO\textsubscript{2} concentration are used to determine various parameters governing leaf photosynthesis capacity. At the low C\textsubscript{i}, Rubisco-limited region of the A-C\textsubscript{i} curve, V\textsubscript{c,max} and R\textsubscript{d} may be solved, as in Xu and Baldocchi (2003), through a best fit of a linear function of C, determined through combining equations [6] and [7]:

\[ A = f'V_{c,max} - R_d \]  \hspace{1cm} [17]

Where

\[ f' = \frac{C - I^*}{C + K_c \left( 1 + \frac{O}{K_o} \right)} \]  \hspace{1cm} [18]

C can represent either C\textsubscript{i} or C\textsubscript{c}, depending on assumptions made regarding the role of g\textsubscript{i} in limiting CO\textsubscript{2} diffusion.

At higher C\textsubscript{c} values, RuBP regeneration is slower than the potential rate of RuBP carboxylation/oxygenation by Rubisco and so limits photosynthesis. The net RuBP-limited CO\textsubscript{2} assimilation rate, A\textsubscript{j}, is expressed by combining equations [6] and [8] as an enzymatic Michaelis-Menten processes whose efficiency diminishes with increasing C:

\[ A_j = \frac{J \left[ C - I^* \right]}{4 \left( C + 2I^* \right)} - R_d \]  \hspace{1cm} [19]

Two fitting procedures were implemented in sequence. The first follows Xu and Baldocchi (2003) and fits A\textsubscript{c} equation [17] for points where C is less than 150 \textmu mol mol\textsuperscript{-1}, and then fits J\textsubscript{max} for equations [10] and [19] for higher values of C using the value of R\textsubscript{d} determined in the first part. The range of points used for the second, high C, half of the analysis is set first as the points where C is greater than 300 \textmu mol mol\textsuperscript{-1}. If this fit is unsatisfactory (RMSE of the estimated A is greater 2 \textmu mol m\textsuperscript{-2}s\textsuperscript{-1}), then the threshold C value of 300 \textmu mol mol\textsuperscript{-1} is incrementally increased until either the RMSE is within the tolerance value (2 \textmu mol m\textsuperscript{-2}s\textsuperscript{-1}) or there are only two remaining points in the A-C\textsubscript{i} curve. This method is applied for various estimates of g\textsubscript{i} to see whether incorporating internal conductance improves the model’s fitness.

The second curve-fitting method follows Sharkey et al. (2007), by simultaneously fitting equations [17] and [19] and finds the best estimates of R\textsubscript{d}, V\textsubscript{c,max}, J, and g\textsubscript{i}. All parameters are temperature-corrected using the values in Table 2-1. There are two main differences from the Sharkey et al. (2007) model: (1) in curves taken here, the TPU limits described in equation [9], are ignored after some preliminary analysis suggested that the A-C\textsubscript{i} curves were not depressed even at very high C\textsubscript{i} values (>1200 \textmu mol mol\textsuperscript{-1}), and (2) all, rather than some, points in each curve are pre-allotted to the A\textsubscript{c} or A\textsubscript{j} regions. The Sharkey method requires the pre-allotment of points to different regions of the curve, which is similar to most A-C\textsubscript{i} fitting methods (Dubois et al., 2007; Ethier and Livingston, 2004; Miao et al., 2009). This pre-allocation can be assisted through analyzing where the transition between A\textsubscript{c} and A\textsubscript{j} regions is located, using equation [20] and assuming the parameter values estimated using the first fitting procedure:

\[ C_{crossover} = \frac{K_c \left( 1 + \frac{O}{K_o} \right) - \frac{8I^*V_c}{J}}{4V_c J - 1} \]  \hspace{1cm} [20]

A semi-exhaustive domain search was implemented, where this crossover concentration (C\textsubscript{crossover}) is allowed to change in steps from 50% to 150% of the value determined from equation [20]. This type of exhaustive search follows other researchers (Dubois et al., 2007; Gu...
et al., 2009), who have established the difficulty of finding best-fit solutions to the simultaneous fitting procedure outlined in Sharkey et al. (2007). The challenge lies in optimizing a problem that has a transition point between two different regimes: most optimization routines cannot move this point, nor can they prevent “state-switching” between local minima from overwhelming the routine. These problems are addressed to some extent by using both light and CO$_2$ response curves to estimate $R_d$, and by investigating results to reduce the risk of model equifinality. Issues in fitting these curves are the subject of much current research (Patrick et al., 2009; Su et al., 2009).

Determining the parameters of the photosynthesis model is important in its own right, but is also used to generate a plant-specific functional dependency to temperature by using and comparing equations [12] and [13]. These parameterized equations, using field collected data, are compared to the standard parameterizations found in Table 2-1, which are derived from more careful laboratory studies.

2.3.1.4 Use of fluorescence to determine gas exchange parameters

The following is a description of the relevant equations to chlorophyll fluorescence, with a focus on verifying that the electron transport rate estimated from chlorophyll fluorescence ($J_f$) is equivalent to the rate derived from gross CO$_2$ assimilation ($J_c$). Much of this nomenclature is from Vankooten and Snel (1990) and is summarized in both the Licor 6400 manual and in other texts (Genty et al., 1989; Warren, 2006).

The absorption of a quantum of light by a molecule of chlorophyll results in transfer of energy from the quantum to the valence electrons of the chlorophyll. The chlorophyll’s excited state is rapidly reverted to its ground level, and the absorbed energy is released to fluorescence, heat, or photosynthetic chemistry:

$$ F + H + P = 1 \quad [21] $$

Where fluorescence ($F$), heat ($H$) and photochemistry ($P$) are given as fractions of the total absorbed quanta (assumed to be 1). $P$ is also known as the quantum yield or efficiency, which decreases with increased light. At a saturating light intensity, then, the chlorophyll photochemistry will not increase, and so $P$ will be zero. $F$ and $H$ will then be at their maximal values: $F_m$ and $H_m$, respectively. If all the de-excitation is indeed through heat and fluorescence at saturating light, then:

$$ F_m + H_m + 0 = 1 \text{, or } H_m = 1 - F_m \quad [22] $$

After assuming that the ratio of heat to fluorescence de-excitation does not change, i.e. that:

$$ \frac{H}{F} = \frac{H_m}{F_m} \quad [23] $$

Then $H = \frac{F(1-F_m)}{F_m}$, and measuring $F$ in non-saturating light conditions and $F_m$ in saturating light conditions allows a solution for both $H$ and $P$:

$$ P = 1 - F + H $$

$$ P = 1 - F + \frac{F(1-F_m)}{F_m} $$

$$ P = \frac{F_m - F}{F_m} \quad [24] $$
If the non-saturating light is non-zero and the leaf is completely adapted to it so that photosynthesis is at steady-state, then

\[ P_{\text{light}} = \frac{F_m' - F}{F_m'} = \Phi_{\text{PSII}} \]  \[25\]

Where the prime implies light-adapted measurements, and \( P_{\text{light}} \), the fraction of absorbed photons used for photochemistry in a light-adapted leaf, is usually written as \( \Phi_{\text{PSII}} \) or \( \Delta F/F_m' \).

The quantum yield of photosynthesis can also be determined from gas exchange measurements, and is given the symbol \( \Phi_{\text{CO}_2} \):

\[ \Phi_{\text{CO}_2} = \frac{A - R_d}{1/\alpha_{\text{leaf}}} \]  \[26\]

Where \( A \) is the assimilation rate, \( R_d \) is the daytime mitochondrial respiration rate (both have units \( \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \)), \( I \) is the incident photon flux density (\( \mu\text{mol m}^{-2} \text{ s}^{-1} \)), and \( \alpha_{\text{leaf}} \) is the leaf absorptance. The actual flux of photons, or the electron transport rate, that drives photosystem II (PS II) is also inferred from chlorophyll fluorescence measurements. It is abbreviated \( \text{ETR} \) (or \( J_f \), the electron transport rate measured through fluorescence) and has units (\( \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \)):

\[ \text{ETR} = \left( \frac{F_m' - F}{F_m'} \right) f_{\text{PSII}} \alpha_{\text{leaf}} = \Phi_{\text{PSII}} f_{\text{PSII}} \alpha_{\text{leaf}} = J_f \]  \[27\]

Where \( f_{\text{PSII}} \) is the fraction of absorbed quanta used by PS II, and is often assumed (by Licor and others) to be 0.5 for C3 plants (and 0.4 for C4 plants). Other authors (von Caemmerer, 2000) use \( f_{\text{PSII}} = 0.48 \) and Laisk and Loreto (1996) give a species-dependent range of \( f \) from 0.42 to 0.60 (their \( Y_{\text{IIm}} \)).

In the non-photorespiratory case (with 2% \( \text{O}_2 \)), the removal of photorespiration allows a comparison between \( J_c \) and \( J_f \) in such a way that the presence or absence of alternate electron sinks (besides PS II) are determined. The value of \( f_{\text{PSII}} \), the fraction of absorbed quanta used by PS II, can be determined as the slope in a graph of the terms of equation [27] rewritten as:

\[ \frac{J_c}{\alpha I} = f_{\text{PSII}} (1 - F_s/F_m') \]  \[28\]

The measurement of \( J_f \) represents total electron transport, and in addition to the electron transport to drive photosynthesis it includes potential “alternate electron sinks” such as nitrate reduction and light-dependent \( \text{O}_2 \) uptake, as summarized and reviewed in Laisk and Loreto (1996) and Caemmerer (2000). Deviations from a one-to-one correlation between \( J_f \) and \( J_c \) are often explained by the use of part of \( J_f \) to reduce these alternate electron receptors. The electron transport rates estimated by both gas exchange and fluorescence have been demonstrated to correlate very closely under non-photorespiratory conditions (i.e., at low \( \text{O}_2 \) partial pressures and various \( \text{CO}_2 \) partial pressures and irradiances) by several authors (Edwards and Baker, 1993; Genty et al., 1989; Ghoshghaie and Cornic, 1994; von Caemmerer, 2000). At low photorespiration levels, one assumes little energy is required for the photorespiratory (PCO) cycle so that (von Caemmerer, 2000):

\[ A = \frac{J_c}{4} \approx \frac{J_c}{4} - R_d \]  \[29\]
2.3.1.4.a Estimating internal conductance: Constant $J$ method

The constant $J$ method for determining internal conductance has been described in detail elsewhere (Harley et al., 1992a; Warren, 2006), but is reviewed briefly here. It uses the following relationships between $J_c$, the electron transport rate determined by gas exchange methods, and $J_f$, the electron transport rate determined by fluorescence. $J_c$ is defined:

$$J_c = \frac{(A + R_d)(4C_c + 8\Gamma^*)}{(C_c - \Gamma^*)}$$  \[30\]

This statement represents the NADPH-limited rate; alternate stoichiometries of the oxygen evolution rate at PS II can yield coefficients of $(4, 9.33)$ or $(4.5, 10.5)$ in place of the $4$ and $8$ in the equation above, respectively. By replacing $C_c$ with $C_i - A/g_i$, $J_c$ is determined as:

$$J_c = \frac{(A + R_d)(4[C_i - A/g_i] + 8\Gamma^*)}{([C_i - A/g_i] - \Gamma^*)}$$  \[31\]

The constant $J$ method assumes that when $A$ is limited by RuBP regeneration at high $\text{CO}_2$, $J$ is constant, and so the response of $A$ to $\text{CO}_2$ depends on $C_c$ and the $\text{CO}_2/O_2$ specificity of Rubisco (Bongi and Loreto, 1989; Warren, 2006). The internal conductance $g_i$ is determined by minimizing:

$$\sum_{i=1}^{n} \frac{(J_\bar{X} - J_i)^2}{n - 1}$$  \[32\]

Where $J_\bar{X}$ is the mean value of $J_c$ for three or more $C_i$ values (at the given $g_i$), and $J_i$ is the value of $J_c$ for each $C_i$. Uncertainties in the constant $J$ method may derive from two effects of high $\text{CO}_2$ measurement conditions: reduced photosynthesis resulting from reaching TPU-regeneration limits and the increased probability of measurement errors from leakage and diffusion of high $\text{CO}_2$ concentrations away from the gas chamber. Finally, this method assumes that $g_i$ is invariant across a large range of $\text{CO}_2$ concentrations, a conjecture partially supported in research on wheat (Tazoe et al., 2009) and partially rejected by studies on sunflower (Vrábl et al., 2009) and the sclerophyllous plant Banksia (Hassiotou et al., 2009).

2.3.1.4.b Estimating internal conductance: Variable $J$ method

The variable $J$ method to determine internal conductance is similar to the constant $J$ technique but assumes measurements are made during conditions where the electron transport rate varies with respect to light or $\text{CO}_2$ concentration (Harley et al., 1992a; Pons et al., 2009; Warren, 2006). This method assumes that the rate of linear electron transport ($J_c$) is a function of gross photosynthesis ($A$), the chloroplast $\text{CO}_2$ concentration ($C_c$) and a given photocompensation point ($\Gamma^*$). This method substitutes the $J_f$ of equation [27] for the $J_c$ of equation [31], by assuming that $J_f$ and $J_c$ have a 1:1 relationship. This equality holds under conditions which can be determined by measuring $J_f$ under a non-photorespiratory setting (i.e., at low $O_2$). The resulting expression for $g_i$ is:

$$g_i = \frac{\frac{A}{C_i} - \frac{\Gamma^* [J_f + 8(A + R_d)]}{J_f - 4(A + R_d)}}{1}$$  \[33\]
The results of these methods based on the electron transport rate can be compared to estimates of \( g_i \) based on the curvature of the A-C\(_i\) curves.

### 2.3.1.5 Stomatal Conductance Model
Gas exchange data recorded during the electron transport fluorescence measurements offer an opportunity to compare and parameterize stomatal conductance models for use in later plant physiological modeling. Because these measurements are taken on different leaves and plants throughout the field region, they supply a record of natural variability to environmental and physiological conditions. Two stomatal models are compared: the “Ball-Berry” model of Collatz et al. (1991), given in equation [34], and its improvements in Leuning (1995), given in equation [35].

\[
g_s = m \frac{A_n RH}{C_s} + b \tag{34}
\]

\[
g_s = a_1 \frac{A_n}{(C_s - \Gamma^*) \left(1 + \frac{D}{D_x}\right)} + g_0 \tag{35}
\]

In the Ball-Berry model, \( RH \) refers to relative humidity at the leaf surface, \( C_s \) refers to the \( CO_2 \) concentration at the leaf’s surface, \( m \) is a slope term, and \( b \) is an intercept referring to a residual (e.g., cuticular) conductance. Similarly, in the Leuning model, \( a_1 \) refers to a slope, \( D \) is the vapor pressure deficit at the leaf surface, \( D_x \) is a parameter, and \( g_0 \) refers to the residual conductance. While not perfect models, due in part to the assumptions and aggregation of complex guard cell functions (Dewar, 1995; Dewar, 2002), these models are commonly used in plant physiological modeling (Daly et al., 2004) and improve upon the more empirical, less feedback-oriented model of Jarvis (1976).

### 2.3.2 Field methods to measure instantaneous photosynthesis
#### 2.3.2.1 Gas exchange measurements
Leaf gas exchange was determined with a portable steady-state photosynthetic system (Licor Li-6400) with an integrated fluorescence chamber head (Licor Li-6400-40). This chamber head has a self-contained light source to control incoming light levels, including the ability to provide a saturating flash of light. The leaf chamber system was calibrated at the beginning, middle, and end of the season against secondary calibration gases that were referenced to standards prepared by NOAA’s Climate Monitoring and Diagnostics Laboratory. The span for water vapor was calibrated with a Licor dew point generator (Li-610). Chamber head gaskets are replaced on a regular basis (approximately monthly).

Leaks from leaf gas exchange chambers occur largely from diffusion of \( CO_2 \) from the atmosphere to the chamber (with low chamber \( CO_2 \) concentrations) or from the chamber to the atmosphere (with high chamber \( CO_2 \) concentrations). Gas exchange measurements reported in the literature are occasionally corrected for leaks and occasionally not, and methods of correction are still under debate. These subjects are reviewed in Flexas et al. (2007). The magnitude of leaks has important consequences in A-C\(_i\) modeling and is of particular importance in determining gas exchange parameters at low \( CO_2 \) concentrations (such as daylight or dark respiration, and the photo-compensation and \( CO_2 \) compensation points, \( I^* \) and \( I_c \), respectively).
and at high CO$_2$ concentrations (such as the onset of phosphorous-limited photosynthesis and internal conductance as determined by the “constant $J$” method). Leak effects and the inconstancy of $\tau$ also limit the effectiveness of the Laisk method of determining $R_d$, as described in Galme et al. (2006).

Tests performed using the leaf chamber system used for all photosynthesis measurements in this chapter suggest that leak effects are negligible. Closed-chamber gasket experiments show low leakage rates (contributing less than 1.2 $\mu$mol m$^{-2}$s$^{-1}$ of apparent respiration at low CO$_2$ concentrations, and between -1 and 1.7 $\mu$mol m$^{-2}$s$^{-1}$ of apparent photosynthesis at high CO$_2$ concentrations). Flexas et al. (2007) show that inert leaves leak less than a closed chamber with fresh gaskets, and so, this work does not correct for leakage. The reduction in leakage from leaves placed in the chamber results from the leaf’s surface roughness, which inhibits diffusion.

2.3.2.2 Fluorescence Measurements
Fluorescence and leaf gas exchange are measured simultaneously in the Licor 6400-40 Leaf Chamber Fluorometer, which contains blue, far red, and red LEDs and two detectors. To detect maximal fluorescence during a brief period when the photosystem is light saturated (at greater than 7000 $\mu$mol m$^{-2}$s$^{-1}$), the fluorometer uses 27 red LEDs and monitors PAR levels using a calibrated light sensor. ETR measurements are taken in four different routines as follows:

1. Measurements are taken in non-photorespiratory conditions (using low 2% O$_2$ air connected to the Licor 6400-40 gas intake as described in its manual) at different light levels to confirm that the electron transport rate measured from fluorescence adequately represents electron transport rates measured from gas exchange. Three leaves were changed with PAR quantum flux changed in the steps: 2000, 1600, 1200, 800, 400 $\mu$mol m$^{-2}$s$^{-1}$; and one leaf was measured with PAR quantum flux in the steps: 150, 250, 450, 650, 850, 1050, 1250, 1450, 1800, 2100, 2400, 2800, 3000, 2500 $\mu$mol m$^{-2}$s$^{-1}$.

2. Under saturating light conditions (often PAR flux of 3000 $\mu$mol m$^{-2}$s$^{-1}$), fluorescence flash measurements are taken to generate maximal electron transport rate (or internal conductance).

3. Under ambient light conditions, fluorescence flash measurements are taken to generate representative instantaneous electron transport rate measurements.

4. Under high CO$_2$ concentrations, ETR measurements are used to determine where the constant $J$ method can be used to generate estimates of internal conductance; these measurements determine in which range of CO$_2$ values $\Phi_{PSII}$ is constant.

2.3.2.3 Light Curve Measurements
A-PAR curves taken throughout the growing season (approximately weekly) generally have photosynthesis estimates taken at PAR values of: [0, 50, 125, 200, 300, 550, 800, 1000, 1400, 1800, 2300, 3000] $\mu$mol quanta m$^{-2}$s$^{-1}$, with up to five and a half minutes separating measurements to ensure a temporary equilibrium is reached. Light curve measurements require a balance between the need to take longer for each measurement point to give the leaf time to equilibrate to the new conditions with the need to reduce the overall time a curve takes – the longer time period of measurement increases overall stress to the leaf and increases the opportunity for temperature or humidity fluctuation. These A-PAR curves are all taken under a reference CO$_2$ concentration of 400 $\mu$mol mol$^{-1}$, which is beneficial because its proximity to atmospheric CO$_2$ conditions eliminates the need to correct for leaks.
A set of A-PAR curves was taken to investigate the Kok effect more closely by increasing the number of low light level measurements, also at the reference CO$_2$ concentration of 400 $\mu$mol mol$^{-1}$. Two A-PAR curves were taken DOY 298 with finely spaced low PAR levels in order to estimate $R_d$ through the Kok method and to investigate the transition to the Kok-dominated region. Here, the PAR values were: [0, 30, 50, 80, 100, 125, 160, 200, 300, 550, 800, 1200, 1700, 2300, 3000] $\mu$mol quanta m$^{-2}$s$^{-1}$, with between three and five minutes separating each measurement. The measurements in this case can be taken slightly more closely together because their proximity reduces the time to equilibrium. An additional A-PAR curve was taken DOY 315 with more PAR values: [0, 20, 30, 50, 70, 90, 115, 140, 160, 200, 300, 550, 800, 1200, 1700, 2300, 3000] $\mu$mol quanta m$^{-2}$s$^{-1}$.

Curves were pre-screened through a combination of visual inspection, initial parameter estimation, and best-fit characteristics of a non-rectangular hyperbola. Curves were rejected if the shape appeared to contain too much deviation from the predicted non-rectangular hyperbola. If the initial estimate of $R_d$ from the fitted non-rectangular hyperbola was negative, the curve was rejected. Curve fits that generated a high sum of square deviations or a relatively low $r^2$ correlation term (less than 0.95) were also rejected.

2.3.2.4 A-C$_1$ Curve Measurements

A-C$_1$ curves were taken throughout the season, within and around the eddy covariance tower on different types of leaves and plants (e.g., rosette leaves, low, mid, and high leaves, on plants before, during, and after flowering). These curves were taken with the general strategy of starting near atmospheric CO$_2$ concentrations, reducing the CO$_2$ in the cuvette in steps, then bringing the CO$_2$ concentration up to some high value before returning to the starting concentration. Most of the curves were taken with the steps: [400, 300, 100, 50, 150, 250, 350, 450, 550, 700, 1000, 1200, 850, 600, 400] $\mu$mol CO$_2$ m$^{-2}$s$^{-1}$. At the end of the growing season six curves were taken with the following steps, to determine whether TPU limits were noticed at the higher CO$_2$ concentrations: [400, 300, 100, 50, 150, 250, 350, 450, 550, 700, 1200, 1600, 2000, 1800, 1000, 850, 600, 400] $\mu$mol CO$_2$ m$^{-2}$s$^{-1}$. At the beginning of the growing season some other concentration sequences were used in order to determine a reasonable method for the rest of the measurements. Leaves were typically given from 200 to 300 seconds to adjust to each CO$_2$ concentration. To the best of the Licor 6400’s ability, leaf temperatures were held constant throughout the curve at a temperature similar to its condition at the start of the curve. Light levels were held constant throughout the measurement period, and were near saturating (most often, at 3000 $\mu$mol quanta m$^{-2}$s$^{-1}$, though occasionally at slightly lower PAR levels: 1900, 2500, or 2700 $\mu$mol quanta m$^{-2}$s$^{-1}$).

Curves were pre-screened by inspection, to remove curves where the measured $A$ for the same CO$_2$ conditions varies too greatly between the beginning and end of the curve. Curves where points showed greater than normal scatter were also removed. Such steps are often necessary in curvature analysis due to the changing chamber temperature, light, humidity, and carbon conditions and occasionally inadequate time for leaf equilibration (Laisk et al., 2002).

2.3.2.5 Laisk method measurements

Measurements to support the Laisk method of determining $I^*$ and $R_d$ were performed on five occasions from September 24, 2008 to November 10, 2008 (Days of Year 268, 286, 292, 298, 315), and once on July 9, 2009 (Day of Year 190). These measurements were made on leaves from the following types of plants (in chronological order): senescing, flowering, rosette on a
flowering plant, flowering, rosette, and flowering. For the first set of measurements, different leaves were used on the same or neighboring plants, and for the rest of the datasets the same leaf was used throughout the measurement period.

2.3.3 Leaf Physiological Characteristics
Over the course of 2008, perennial pepperweed leaf samples were collected at the Sherman Island research site, and then brought to the laboratory where leaf area was measured with an optical area meter (Li-3100, Li-Cor Lincoln, NE, USA). Subsequently, leaf samples were dried at 65°C for 48 hours and weighed to determine leaf mass per dry area (LMA) and fresh water content (FWC), or water weight per wet leaf weight. Dried and ground leaf samples were then analyzed for carbon and nitrogen content (percent of dry weight) via elemental analyzer/mass spectrometry. The leaf economic spectrum (Shipley et al., 2006) was explored using the %N and LMA values from perennial pepperweed, and compared to the published GLOPNET leaf economics dataset (Wright et al., 2004).

The leaf absorptance was characterized using an external integrating sphere (Licor 1800-12) with attached fiber optic sensor (Ocean Optics Inc., Dunedin, FL). This sensor has a range from 340 to 1017 nm, with approximately 0.3 nm precision. Its output was recorded using the Ocean Optics OOIBase32 software. On eight occasions, six to thirteen fresh leaves were measured in the integrating sphere for transmittance and reflectance so that leaf light absorptance could be determined by difference. Samples were transported to the integrating sphere in a dark cooler and analyzed within four hours of clipping. In each measurement, a reference and dark value are stored prior to determining the transmittance and reflectance. The leaf's top side is considered as receiving the incident light. Absorptance in the Licor 6400 LED red (625-700 nm) and blue (450-495 nm) range is presented.

2.4 Results
2.4.1 Leaf Physiological Characteristics
Leaf physiological characteristics are presented prior to the results from the leaf gas exchange analysis. The fresh water content of leaves tends to decrease through the season, while the dry leaf mass per area of leaves tends to increase through the season as more leaf structural components are built (Figure 2-1), though this pattern is less clear for leaves clipped in 2009 than in 2008. The highest values of leaf nitrogen (and lowest C/N ratios) also occur at the beginning of the growing season. Percent nitrogen ranged from 1.75% to 5.58% on a dry mass basis or 0.28% to 1.08% on a fresh mass basis. Percent carbon ranged from 34.86% to 43.53% on a dry mass basis or 4.49%-20.05% on a wet mass basis. The carbon-nitrogen ratio ranges from 6.71 to 24.35. The fresh water content ranged from 53-89%, and the dry leaf mass per area ranges from 0.003 to 0.025 g/cm².
Figure 2-1: Time series of leaf characteristics (left to right, top then bottom): N%, LMA of CN samples, Daily average LMA, C%, C/N ratio, and Daily average fresh water content.

When compared to the GLOPNET dataset (Figure 2-2), pepperweed at Sherman Island appears to be on or near the optimal edge of the leaf economic spectrum with respect to nitrogen content. Pepperweed has similar characteristics as other herbaceous species, as well as deciduous broadleaf species (tree distinctions not shown), as indicated by the overlapping 50% confidence interval ellipses.
Leaf nitrogen plotted against LMA at Sherman Island, compared to the plant types in the GLOPNET database (Wright et al., 2004).

Leaf absorptance in the red and blue wavelengths was determined by integrating sphere to be roughly constant through the season (and through each plant’s canopy). Pepperweed averaged 91.00 (+/−1.09) % absorptance in the red range (625-700 nm), and 88.72 (+/−1.48) % absorptance in the blue range (450-495 nm).

2.4.2 Kok method results
The three A-PAR curves with a high number of low PAR values are presented (Figure 2-3). These curves indicate a steeper slope at low light levels, indicating the presence of the Kok effect.
Figure 2-3: A-Par Curves from DOY 298 and DOY 315 to assess Kok effect and find estimates of $R_d$. Non-rectangular hyperbolae are fit to each curve, for points where PAR is greater than 45 $\mu$mol m$^{-2}$s$^{-1}$. (a) shows whole curve, (b) zooms into region near Kok effect, where low-PAR values are governed by a steeper slope, to be investigated in this section.

First, modeling in the lower-light region is used to determine the transition point between a steep, low-light influenced region (where the ‘Kok effect’ dominates), and the region where the initial slope can be extended back to the y-axis to determine $R_d$. For example, setting the transition point at each PAR measurement and fitting a linear regression to each region above and below this point and comparing the total RMSE gives, for the afternoon curve (DOY 298), the set of results in Figure 2-4. In this case the model with a transition PAR of 50 $\mu$mol quanta m$^{-2}$s$^{-1}$ gives the lowest total RMSE.

The “true” transition point, however, may occur at an intermediate point, between measurements, so a more analytical approach is to find the transition point which minimizes overall RMSE. The fitting algorithm was to manually increment the transitional PAR and to find the values of the two slopes and of photosynthesis at the transition point, which minimizes RMSE at that transitional PAR level. The results of this method for each A-PAR curve are presented in Figure 2-5, and the transition point which minimizes overall RMSE is then used with Equation [14]. The quantum yield of RuP$_2$ regeneration, $V_j$, from Equation [14], is determined from the $A$ and $C_i$ values from measurements taken at the PAR levels between the transition PAR and 200 $\mu$mol quanta m$^{-2}$s$^{-1}$. The value of $R_d$ which minimizes the error of the slope of $V_j$ over this range of PAR values is considered the “true” level of daylight respiration.
Figure 2-4: Kok effect region of three A-Par curves fit in two linear sections. The curves are numbered in chronological order: (1) Oct 24, 2008, morning, (2) Oct 24, 2008, afternoon, (3) Nov 10, 2008, mid-day.

Figure 2-5: The effect of the PAR transition point on various parameters. The upper left plot (a) shows the effects of the choice of PAR transition on $R_d$. Upper right (b) shows how the overall RMSE changes with the choice of transition point, with the discontinuities arising from the shift of measurement points from one linear region to the next. The lower left plot (c) shows the transition of the slopes of the two linear fits through the range of PAR transition points. The lower right (d) shows the value of photosynthesis at the transition point through the range of PAR transition points.
The transition PAR values for each case were 61.5 μmol quanta m\(^{-2}\)s\(^{-1}\) (DOY 298, AM case), 53.5 μmol quanta m\(^{-2}\)s\(^{-1}\) (DOY 298, PM case), and 31.5 μmol quanta m\(^{-2}\)s\(^{-1}\) (DOY 315). Choosing a value of 45 μmol quanta m\(^{-2}\)s\(^{-1}\) as a transition point for the Kok effect for the rest of the season’s A-PAR curves maximizes the number of points used while constraining the steep slope with data from the lowest light levels. Estimates of \(R_d\) in the range of chosen transition points between 31 and 61.5 45 μmol m\(^{-2}\)s\(^{-1}\) suffer less from mis-estimating the transition point than in other transition point regions. Because most of the A-PAR curves have a measurement at 50 μmol quanta m\(^{-2}\)s\(^{-1}\), it is appropriate to include that point as the minimum PAR value for fitting the Kirschbaum and Farquhar (1987) method.

The curve-specific transition PAR values are used when adjusting \(R_d\) to find the best-fit slope of \(V_j\) to PAR (Figure 2-6a), and are compared to results when the lower transition PAR value is 45 μmol quanta m\(^{-2}\)s\(^{-1}\) (Figure 2-6b). In both cases, the upper PAR value used for this regression is the measurement at 200 μmol quanta m\(^{-2}\)s\(^{-1}\).

![Figure 2-6: Best fit slope for \(V_j\) vs. PAR for three A-PAR curves.](image)

This analysis of three higher-resolution A-PAR curves reveals evidence of the Kok effect at low light levels, and suggests that using a transition PAR level of 45 μmol m\(^{-2}\)s\(^{-1}\) is sufficient for estimating \(R_d\) while capturing the Kok effect. Estimates of \(R_d\) for these three leaves were:

(a) 1.42 μmol m\(^{-2}\)s\(^{-1}\) (with transition PAR of 45 μmol m\(^{-2}\)s\(^{-1}\)) or 0.964 μmol m\(^{-2}\)s\(^{-1}\) (with transition PAR of 61.5 μmol m\(^{-2}\)s\(^{-1}\)), for the mid-plant leaf measured in the early morning (DOY 298), with an average temperature of 16 °C.

(b) 6.29 μmol m\(^{-2}\)s\(^{-1}\) (with transition PAR of 45 μmol m\(^{-2}\)s\(^{-1}\)) or 6.48 μmol m\(^{-2}\)s\(^{-1}\) (with transition PAR of 53.5 μmol m\(^{-2}\)s\(^{-1}\)), for the rosette leaf measured in the mid-afternoon, (DOY 298), with an average temperature of 30 °C.

(c) 4.43 μmol m\(^{-2}\)s\(^{-1}\) (with transition PAR of either 45 μmol m\(^{-2}\)s\(^{-1}\) or 31.5 μmol m\(^{-2}\)s\(^{-1}\)), for the rosette leaf measured in the late morning, (DOY 315), with an average temperature of 22 °C.

Finally, estimates of \(R_d\) from the lower-resolution A-PAR curves taken through the season can be analyzed to determine temperature and leaf-type relationships. Results from this process are presented here. Each curve is analyzed using the two methods for determining \(R_d\) while accounting for the Kok effect: (1) using the intercept of the initial slope of the A-PAR curve for points where PAR is between 45 and 200 μmol m\(^{-2}\)s\(^{-1}\), and (2) applying the Kirschbaum and Farquhar (1987) method of selecting \(R_d\) based on the best fit of \(V_j\). This second method is applied twice, once by assuming that \(I^*\) at 25°C is 25 μmol m\(^{-2}\)s\(^{-1}\), and again by assuming it is 45 μmol m\(^{-2}\)s\(^{-1}\). The insensitivity of these methods to \(I^*\) and the similarity of their
results are both demonstrated in Figure 2-7. Not shown are additional comparisons between $R_d$ estimated when $I^*$ at 25ºC is assumed to be either 37.43 or 55 μmol m$^{-2}$s$^{-1}$; in both cases the resulting $R_d$ is very similar to those shown in Figure 2-7. In Figure 2-6 where an estimate of $I^*$ at 25ºC is required for estimating $R_d$ from the A-PAR curves, the value of 37.43 μmol m$^{-2}$s$^{-1}$ is used, for consistency with Bernacchi et al. (2002).

![Figure 2-7: Similarity of $R_d$ estimates using two techniques. Two $I^*$ estimates are considered for the Kirschbaum and Farquhar (1987) method. Results from all 31 light curves shown; data from the 14 ‘good’ light curves show similar patterns.](image)

2.4.3 Laisk Method Analysis

These datasets are analyzed by the four methods described in the methods section above, where linear and non-rectangular hyperbola models are used to search for the $(I^*, R_d)$ point that best fits the data. Each successive method is considered “more advanced” than the one before, so the results are presented in order from “most naïve” to “most complex”. All the optimizations are performed using a sequential quadratic programming method within the medium-scale optimization routine of the fmincon function in Matlab (by Mathworks, Inc.).

Method (1), where a linear fit is applied to each set of data, where $C_i$ is less than 150 ppm, is the most “basic” fitting method. While often in the literature these lines are fit only through points with $C_i$ less than 100 ppm, it seemed reasonable with this dataset to include more points in the data-fitting process. Data and these initial linear fits are shown in Figure 2-8. The parameters $I^*$ and $R_d$ could be estimated through visual inspection, but it is apparent that this process will generate a wide range of possible solutions.
Figure 2-8: Estimating $I^*$ and $R_d$ through the Laisk approach, Method (1). A straight line is fit to each PAR-level for points where $C_i < 150$ ppm. Where curves had less than two points meeting this criterion, no line was generated.

Method (2), where estimates of $I^*$ and $R_d$ are made by forcing an intercept between the linear regressions of each PAR curve, is presented in Figure 2-9. This method suggests a range of $I^*$ values between 0 and 56.3 μmol mol$^{-1}$ and $R_d$ values between 1.82 and 5.62 μmol m$^{-2}$ s$^{-1}$, where each parameter has been normalized to 25°C using the temperature equations parameterized in Table 2-1. The root-mean-square errors associated with each linear fit are only slightly increased by forcing an intercept.

Figure 2-9: Estimating $I^*$ and $R_d$ through the Laisk approach, Method (2). Straight lines are fit to each PAR-level for points where $C_i < 150$ ppm, under the constraint that these lines share a common intersect, which is the point $(I^*, R_d)$, normalized to 25°C. The overall root-mean-square error is minimized.

The third method for fitting the Laisk datasets is to fit a non-rectangular hyperbola to each curve without regard to a common intercept. This method is presented in Figure 2-10, and like method 1 would require some kind of inspection technique to determine the approximate range of $(I^*, R_d)$ where the curves intersect.

Figure 2-10: Estimating $I^*$ and $R_d$ through the Laisk approach, Method (4). A four-parameter non-rectangular hyperbola is fit to each PAR-level (for all points) by minimizing the root-mean-square error of each curve.

The fourth method for fitting the Laisk datasets forces a common intersect for each set of four PAR levels. This method minimizes the overall root-mean-square error of the data to the
four fitted curves for each day’s dataset. The data and their fits are presented in Figure 2-11, for the case where $I^*$ is initially set to 36 μmol mol$^{-1}$.

Figure 2-11: Estimating $I^*$ and $R_d$ through the Laisk approach, Method (5). A four-parameter non-rectangular hyperbola is fit to each PAR-level (for all points) under the constraint that these lines share a common intersect, which is the point ($I^*$, $R_d$), normalized to 25°C. The optimization minimized the overall root-mean-square error of each set of curves. This figure presents results when the initial guess of $I^*$ is 36 μmol mol$^{-1}$.

The optimization routine used to determine the best-fit parameters displayed in Figure 2-11 is sensitive to its initial conditions. To determine the range of estimated parameters, a test of the optimization scheme was conducted upon the five datasets from 2008, where the initial guess of $I^*$ was varied between 0-100 μmol mol$^{-1}$ (in unit intervals). The set of 101 “optimal” non-rectangular hyperbolae fit to each dataset are presented in Figure 2-12, where it is clear that the widest spread in the fitted curves occurs at high or low ranges of $C_i$ where there are little or no data points to constrain the curve.

Figure 2-12: Multiple "optimal" non-rectangular hyperbolae fit to the datasets; for each date the curves are forced to intersect at ($I^*$, $R_d$).

The range of $R_d$ and $I^*$ values determined through this set of 101 optimization runs is displayed in Figure 2-13. The range of optimal $I^*$ values is wider than the range of $R_d$ values. The root-mean-square error for each estimate of $R_d$ and $I^*$ is shown in Figure 2-14.
Figure 2-13: Multiple "optimal" best-fit parameter values (from different initial estimates of $I^*$). The ten values for each dataset that give the lowest root-mean-square error are circled.

Figure 2-14: The objective function (root-mean-square error) as a function of parameter estimates ($I^*$ and $R_d$).

The “best” linear fits are shown in Figure 2-15. The measurements from September 24, 2008, were fit using all $C_i$ values less than 170 $\mu$mol mol$^{-1}$ so that each set of measurements could have its linear fit contain at least three data points. The other datasets had linear fits applied to all data where $C_i$ is less than 110 $\mu$mol mol$^{-1}$, in order to include some data where $C_i$ is just greater than 100 $\mu$mol mol$^{-1}$, the traditional cut-off concentration used by other researchers.
September 24, 2008 dataset uses $C_{i_{\text{max}}}=170 \ \mu\text{mol mol}^{-1}$, others use $C_{i_{\text{max}}}=110 \ \mu\text{mol mol}^{-1}$. Data where PAR=550 on Oct 12, 2008 and where PAR=550 on Nov 10, 2008 excised because of its greater scatter than data at other light levels.

In each case (for 2008 datasets), fitting the curves using a non-infinite value of internal conductance gave a higher root-mean-square error than simply fitting curves where $C_c$ is assumed to equal $C_i$ (Figure 2-16).

For $g_i$ less than approximately 0.05 mol m$^{-2}$s$^{-1}$, the Laik curves lose physical meaning, as $C_c$ becomes negative.

The results of this Laik analysis are presented in Table 2-2; $I^*$ has an average, temperature adjusted value of 43.5 $\mu$mol m$^{-1}$, and $R_d$ has an average, temperature-adjusted value of 3.06 $\mu$mol m$^{-2}$s$^{-1}$. The role of any internal resistance to $\text{CO}_2$ diffusion is negligible, as assuming a value of $g_i$ offers no improvement to the fitting methods.
2.4.4 A-PAR results

The parameters from the A-PAR curves are displayed over the season in Figure 2-17. The average value of $\Phi$, the quantum yield of electron transport, is 0.036. There is a great range in the curvature parameter. There is no apparent correlation between seasonality or temperature and the parameters, though the rosette leaves indicated in the lower left plot do have uncharacteristically high light compensation points. In all cases, the maximum (asymptote) value of photosynthesis ($A_{\text{max}}$) is greater than the rate of photosynthesis at the highest light level measured, 3000 $\mu$mol quanta m$^{-2}$s$^{-1}$ ($A_{3000}$). The respiration values ($R_d$) are analyzed in more detail when combined with the values from the $A-C_i$ curves in a later section. The average leaf temperature during measurement is given in the figure for convenience and comparison.
Figure 2-17: Time series of parameter estimates from fourteen light-response curves taken under field conditions on perennial pepperweed.

2.4.5 A-C\textsubscript{i} Results

The \( A-C_i \) curves were analyzed using the initial slope method to generate estimates of \( V_{cmax} \) and \( R_d \), before determining \( J_{max} \) using the high-\( C_i \) data. These estimates are then used to determine the temperature response of these parameters (Figure 2-18). Mean leaf temperature is correlated to the estimate of \( V_{cmax} \) with \( r^2 = 0.69 \) (\( n=43 \), \( p<0.001 \)). The Arrhenius model adequately fits the data with \( r^2 = 0.707 \), while the two additional parameters of the unconstrained or constrained Peaked model only marginally increase \( r^2 \) to 0.711. F-tests of the fitted models suggest that the literature value of \( H_a \) cannot be rejected and that the peaked model cannot be recommended over the Arrhenius model (at \( P=0.05 \) confidence). A t-test on the unconstrained fit to \( H_a \) shows that the literature value of \( H_a \) cannot be rejected (as \( P=0.27 \)).

With the leaf absorptance determined in the integrating sphere, the terms following the incident light, \( Q \), in equation [11], become 0.3825 (i.e., the useful quanta for photosystem II, \( Q_2 \), is 38.25% of incident irradiance \( Q \)). This conversion is used in determining \( J_{max} \) from the \( A-C_i \) curves (equation [10]).
Figure 2-18: Response of $V_{c,max}$ to leaf temperature. Two variants each of two models are fit to the data: The Arrhenius model is fit with and without constraining activation parameter $H_a$ to the estimate of 65.33 kJ mol$^{-1}$ from Bernacchi et al. (2001), and the peaked model is fit with and without setting $H_d$ to 200 kJ mol$^{-1}$, as commonly assumed (Medlyn et al., 2002). The models are fit without including the outlier at lower right, which is from an older leaf in a plant at a canal’s edge. $H_a$ and $H_d$ have units kJ mol$^{-1}$. The two circled points are data from 2009.

The response of $J_{max}$ to temperature is much weaker than the dependence of $V_{c,max}$ (Figure 2-19), as they are correlated at $r^2=0.14$ (p=0.0136, n=43). $J_{max}$ values range from 162 μmol m$^{-2}$ s$^{-1}$ at 20.7°C to 341 μmol m$^{-2}$ s$^{-1}$ at 30.3°C, and the Arrhenius model predicts that the 50% confidence range of $J_{max}$ at 25°C is 184-260 μmol m$^{-2}$ s$^{-1}$. A t-test on the unconstrained fit to $H_d$ shows that the literature value of $H_d$ cannot be rejected (as P=0.106). The ratio between $J_{max}$ and $V_{c,max}$ is similar to the 1.67 reported in Medlyn et al. (2002), as shown in Figure 2-20.
Figure 2-19: Response of $J_{\text{max}}$ to leaf temperature; the two circled points are from 2009.

Figure 2-20: Comparison of $J_{\text{max}}$ and $V_{c,\text{max}}$. Both values are temperature-normalized to 25°C. No significant difference was found between the fit found by Medlyn et al. (2002) and the best-fit to this dataset. The two darkened points are from 2009.

The response of $R_d$ to temperature is presented in Figure 2-21, which combines results from the A-C$_i$ and A-PAR analyses. The A-PAR results suggest slightly higher estimates of $R_d$ than the A-C$_i$ results, and the A-PAR results are more closely correlated to temperature ($r^2=0.454$, $p=0.0082$, $n=14$) than the A-C$_i$ results ($r^2=0.02$, $p=0.3$, $n=43$), which have a negligible correlation. The correlation between the combined modeled $R_d$ and temperature is slight ($r^2=0.089$, $p=0.027$, $n=57$).
Testing the A-Ci models by incorporating a term for internal conductance does not ever increase model fitness. Incorporating the internal conductance changes the curvature of the dataset, and so it may be hard to discover improvements through such a rough fitness metric as the root-mean-square error. Figure 2-22 presents the results of this analysis by showing the reduction in the error term as $g_i$ heads towards infinity, and also the average improvement in each stepped increase of internal conductance. Many more intermediate values of internal conductance were modeled, with results consistent to those presented.
Figure 2-22: Response of $A$-$Ci$ curve model fitting to imposed internal conductance. Each box has bounds at the lower and upper quartile, with the interior line drawn at the median value, and whiskers contain the most extreme values within 1.5 times the interquartile range. Outliers are marked with a ‘+’. In every individual curve case, the root-mean-square error is lower if given a $g_i$ of 1000 (i.e., near-infinite) than a lower $g_i$.

In no case was significant reduction in photosynthesis discovered at the high range of CO$_2$ concentrations, so the TPU-limiting case (equation [9]) is ignored. The time series of results from the $A$-$Ci$ model are presented in Figure 2-23. While in no case is the relationship between time of season and parameter value particularly strong (all $r^2$ estimates are less than 0.6), there is some evidence that $V_{c,max}$ peaks towards the end of the summer, when the transition between $A_c$ and $A_i$ occurs at a minimum $C_i$ range. $J_{max}$ and $R_d$ show slight tendencies to increase through the season.
Figure 2-23: Time series of parameters from A-Ci modeling. Filled-in squares are data from 2009, all others from 2008. Fitting $V_{\text{a,max}}$ and $C_{\text{crossover}}$ with a quadratic provided a significant (P<0.05, F-test) improvement over the linear model.

2.4.6 ETR Results
2.4.6.1 Non-photorespiratory conditions (low O$_2$)
Four light response curves were taken under low O$_2$ conditions. The degree of photorespiration is evident from Figure 2-24, which presents light response relationships from neighboring plants under atmospheric and 2% O$_2$ concentration conditions for three of the curves. The relationship between $\Phi_{\text{PSII}}$ and $\Phi_{\text{CO2}}$ is also presented, and is shown to be linear, with a slope of 8.6, which is similar to results in Genty et al. (1989).

It is clear from the middle panel (top row) that there was a measurement problem in one of these measurement sets. The reduced assimilation rate at high light levels derives from inadequate flow of low O$_2$ air and intake of ambient air instead. The problem was fixed between the 2$^{nd}$ and 3$^{rd}$ measurement points (at 1600 and 1200 $\mu$mol quanta m$^{-2}$s$^{-1}$, respectively). Despite this measurement error, the slopes of the $\Phi_{\text{PSII}}$ / $\Phi_{\text{CO2}}$ relationship are relatively constant through the different sets of measurements. In the analyses that follow, these first two erroneous measurement points are removed from consideration.
Figure 2-24: Light response curves and $\Phi_{PSII}/\Phi_{CO2}$ relationship under low O$_2$ (2%) at Sherman Island from three sets of measurements. The first two points in the middle graph seem to have been taken under photorespiratory conditions due to errors in maintaining a constant and suitably high flow of low-O$_2$ air. The left-most plots are for a 28" tall brown-topped (i.e., senescing) plant, southwest of the tower enclosure on a leaf 12" off the ground. The middle plots are for a 28" white-topped (i.e., flowering) plant, 15 m west of the tower enclosure on a leaf 4" off the ground. The right-most plots are for another 28" flowering plant, 15 m west of the tower enclosure on a leaf 15" off the ground. Temperature and humidity conditions for each measurement are provided.

The parameter $f_{PSII}$, the fraction of absorbed quanta used by PSII, is determined for each dataset as shown in Figure 2-25 by fitting equation [28]. Best-fit values of $f_{PSII}$ range from 0.27 for the July 13, 2009, dataset, to 0.45 for the August 19, 2008, dataset. For comparison, the $f_{PSII}$ values of Laisk and Loreto (1996) range from 0.42 (for Vigna, a pea or bean genus) to 0.60 (for Tilia, a genus that includes the linden tree). It is possible that the higher temperatures or some other measurement condition accounts for the lower estimate of $f_{PSII}$ for the leaf sampled July 13, 2009. This change could also result from some as-yet unknown seasonality.

Estimates of $f_{PSII}$, the portion of quanta used by PSII, are sensitive to $R_d$. Figure 2-26 presents this sensitivity, based on equation [28], where $J_c$ is determined using three different sets of $R_d$ estimates. First, $R_d$ is assumed to be the temperature-adjusted value determined from the A-C$_i$ and A-PAR (Kok) methods, and then estimates of $J_c$ are bounded by assuming lower and upper errors to this temperature-adjusted value of $R_d$ of 1.5 $\mu$mol m$^{-2}$ s$^{-1}$. The dataset-averaged estimates of $f_{PSII}$ range from 0.39 to 0.47 under these different assumptions for $R_d$. 

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Figure 2-25: Fitting data to derive $f_{PSII}$ from equation [28]. It is possible that the higher measurement temperatures of July 13, 2009, may account for the change in slope relative to the other datasets.

Figure 2-26: Investigating the sensitivity of $f_{PSII}$ on $R_d$. The three sets of data come from different estimates of $R_d$: The temperature adjusted set is used (in set two) and bounds are given by applying a 1.5 $\mu$mol m$^{-2}$s$^{-1}$ error on $R_d$.

For the measurements at Sherman Island, estimates of $J_f$ and $J_c$ (derived from equation [29]) are pooled between the four measurement sets, and have a correlation of $r^2=0.74$ with all points included (Figure 2-27), and a slope of 1.36 (or 1.1 if forced through the origin). Excluding points where PAR is greater than 1500 $\mu$mol m$^{-2}$s$^{-1}$ generates a correlation of $r^2=0.78$ and a slope of 1.24 (or 1.02 if forced through the origin). These measurements are created by assuming $R_d$ is equal to the temperature-adjusted value determined from the Kok-effect method.
2.4.6.2 Internal conductance; Variable $J$ results

Results from the “variable $J$” method of determining $g_i$ are presented in Figure 2-28, which demonstrates, as predicted from the non-photorespiratory work above, that the method is unstable particularly for measurements with higher PAR values. These measurements often lead to negative estimates of $g_i$ (fully half of all measurement points generate a negative value for $g_i$). The estimated electron transport rate for measurements under higher light conditions tends to be lower than under lower light conditions (Figure 2-28). While the method is sensitive to the various input parameters, such as $I^{*}$, $R_d$, and $f_{PSII}$, no reasonable combination of changes to these parameters could generate a substantial fraction of positive estimates for $g_i$, nor could they be used to generate a consistent estimate of $g_i$ across the dataset.

2.4.6.3 Internal conductance; Constant $J$ method results

The $A-C_i$ and $J_f-C_i$ relationships are shown in Figure 2-29 for the three cases where fluorescence-based estimates of $J_f$ were taken. These relationships demonstrate where the constant $J$ method of deriving $g_i$ can be applied: $\Phi_{PSII}$ is roughly constant when $C_i$ is greater than 900 $\mu$mol mol$^{-1}$. Therefore, while the first leaf sampled did not reach high enough values of $C_i$ to determine a
constant $J$, two others do. This high value of $C_i$ limits the number of curves available to assess $g_i$ using this method. Six curves (including the two presented here) contain more than two points in this range of $C_i$ values to meet this criterion. Only two of these curves yield estimates of $g_i$, as indicated in Figure 2-30, and the others find that an infinite internal conductance is the best fit to the model. Figure 2-30 also demonstrates that the method’s objective function is not steep, and so its results contain less confidence than other methods. Additionally, a sensitivity analysis to the input estimate of $I^*$ in the two curves yielding a $g_i$ estimate indicates that a 10% reduction or addition to $I^*$ (from 4.35 Pa) changes the estimate of $g_i$ by 20-25% or 30-50%, respectively.

Figure 2-29: Net photosynthesis, quantum efficiency, and fluorescence-based electron transport rates over range of intercellular CO$_2$ concentrations for three leaf samples at Sherman Island site (*Lepidium latifolium*).
2.4.7 Stomatal conductance results

Using the gas exchange dataset collected while generating estimates of electron transport rates for the variable $J$ method of determining $g_i$ allows an analysis of stomatal conductance. This analysis is slightly skewed towards conditions where photosynthesis is maximal, since the measurement light levels were often relatively high. Measurements were taken for a range of leaf types and environmental conditions, and span the growing season of 2008. Fits of the two stomatal conductance models to this dataset are presented in Figure 2-31, which demonstrates that the Leuning (1995) model outperforms the Ball-Berry (Collatz et al., 1991) model. Neither model captures the relatively high stomatal conductance at some of the measurements with lower vapor pressure deficit. Light level and temperature are not as important as vapor pressure deficit in governing stomatal response to the environmental conditions (residuals to the fitted models were not as significantly correlated to these parameters as to VPD).
Figure 2-31: Stomatal conductance: fitting the Ball-Berry (Collatz et al., 1991) and Leuning (1995) models. The fit of these models in different vapor pressure deficit ranges is presented for comparison.

2.4.8 Summary
A summary of the parameters determined in this chapter is provided in Table 2-3. The estimates of \( V_{c,max}, J_{max}, \) and \( R_d \) at 25°C differ from those provided in this chapter’s introduction because the estimates in this table derive from the model’s best fit procedure (and the error range indicates the bounds where 50% of the estimates are likely to fall), rather than the re-normalized parameters summarized previously. Although the temperature modeling does not tend to generate significantly different parameter values than using the standard parameterization from Table 2-1, the estimates of the Arrhenius parameter \( H_a \) for each are provided for completeness. In this table the standard error of the Leuning slope (for stomatal conductance) and for the three \( H_a \) terms derives from traditional error estimates of the slope of a linear regression. The standard errors of \( \Phi, I^\alpha, \) and leaf absorptance are the sample standard deviation.
2.5 Discussion

2.5.1 Context

The results presented above represent a broad field survey of the gas exchange processes and leaf characteristics that govern photosynthesis in *Lepidium latifolium*, or perennial pepperweed. The survey reveals a robust photosynthetic infrastructure, with high capacity for incorporating carbon, higher than expected stomatal conductance at lower humidity levels, and high leaf nitrogen levels that may explain one key to its success in crowding out other species. Provided in this section is a discussion of these results, placing them where possible into a comparative context. I also discuss sources of uncertainty in these measurements and models, and offers suggestions for improvement by future researchers.

A number of the species reviewed by Wullschleger (1993) have comparable \( V_{c,max} \) and \( J_{max} \) values to *L. latifolium*, whose mean parameter values (here adjusted to 25°C) are found 113.3 and 218.6 \( \mu \text{mol m}^{-2}\text{s}^{-1} \), respectively. Beet plants (*Beta vulgaris*) have parameters of 194 (\( V_{c,max} \)) and 329 (\( J_{max} \)) at PAR of 3000 \( \mu \text{mol m}^{-2}\text{s}^{-1} \) and temperature 30°C, or 129 (\( V_{c,max} \)) and 226 (\( J_{max} \)), at PAR of 2500 and 25°C temperature. The annual and herbaceous White Goosefoot (*Chenopodium album*) was found to have \( V_{c,max} \) ranging from 103 to 148 and \( J_{max} \) ranging from 227 to 269, depending on measurement conditions. The weedy rough cocklebur plant (*Xanthium strumarium*) has parameter values of 144 (\( V_{c,max} \)) and 302 (\( J_{max} \)). The desert shrub Brittlebush (*Encelia farinosa*) was found to have parameters 182 (\( V_{c,max} \)) and 264 (\( J_{max} \)), and the desert five-spot *Malvastrum rotundifolium* has parameters of 186 (\( V_{c,max} \)) and 372 (\( J_{max} \)). The perennial grass *Festuca arundinacea* has parameters of 118 (\( V_{c,max} \)) and 226 (\( J_{max} \)). Measurements of cotton (*Gossypium hirsutum*) and soybean (*Glycine max*) indicate parameters in this range, as do the creosote bush (*Larrea divaricata*), the evergreen oleander bush (*Nerium oleander*), rice (*Oryza sativa*), the Southwestern-ranging Fremont cottonwood (*Populus Fremontii*), two sunflower samples (*Helianthus annuus* and *petiolaris*), and the white clover (*Trifolium repens*). Only a few species in the Wullschleger (1993) review have higher values of \( V_{c,max} \) and \( J_{max} \) than

<table>
<thead>
<tr>
<th>Fitted Parameters</th>
<th>Value</th>
<th>50% Error range or standard error</th>
<th>Units</th>
<th>Description/Reference/Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>( V_{c,max}(25^\circ C) )</td>
<td>113.3</td>
<td>92.8-131.2</td>
<td>( \mu \text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1} )</td>
<td>From 41 ( A-C ) curves</td>
</tr>
<tr>
<td>( J_{max}(25^\circ C) )</td>
<td>218.6</td>
<td>183.6-259.9</td>
<td>( \mu \text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1} )</td>
<td>From 41 ( A-C ) curves</td>
</tr>
<tr>
<td>( R_d(25^\circ C) )</td>
<td>2.06</td>
<td>1.93-3.53</td>
<td>( \mu \text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1} )</td>
<td>From 41 ( A-C ) curves and 14 ( A-PAR ) curves</td>
</tr>
<tr>
<td>( H_a ) for ( V_{c,max} )</td>
<td>50.58</td>
<td>( \pm 4.83 )</td>
<td>kJ mol(^{-1})</td>
<td>From 41 ( A-C ) curves</td>
</tr>
<tr>
<td>( H_a ) for ( J_{max} )</td>
<td>13.05</td>
<td>( \pm 4.93 )</td>
<td>kJ mol(^{-1})</td>
<td>From 41 ( A-C ) curves</td>
</tr>
<tr>
<td>( H_a ) for ( R_d )</td>
<td>27.51</td>
<td>( \pm 10.31 )</td>
<td>kJ mol(^{-1})</td>
<td>From 41 ( A-C ) curves and 14 ( A-PAR ) curves</td>
</tr>
<tr>
<td>( \Phi )</td>
<td>0.036</td>
<td>( \pm 0.008 )</td>
<td>( \mu \text{mol CO}_2 \text{ \mu mol}^{-1}\text{ quanta} )</td>
<td>Quantum yield, from 14 ( A-PAR ) curves</td>
</tr>
<tr>
<td>( I^* )</td>
<td>4.35</td>
<td>( \pm 1.21 )</td>
<td>Pa</td>
<td>From 6 Laisk datasets</td>
</tr>
<tr>
<td>Leuning ( g_c ), ( D_c ) term</td>
<td>1.0</td>
<td>n/a</td>
<td>kPa</td>
<td>From 140 ETR measurements</td>
</tr>
<tr>
<td>Leuning ( g_c ), slope</td>
<td>18</td>
<td>( \pm 0.85 )</td>
<td>n/a</td>
<td>From 140 ETR measurements</td>
</tr>
<tr>
<td>absorptance, red</td>
<td>91</td>
<td>( \pm 1.09 )</td>
<td>%</td>
<td>From 8 collection campaigns</td>
</tr>
<tr>
<td>absorptance, blue</td>
<td>88.72</td>
<td>( \pm 1.48 )</td>
<td>%</td>
<td>From 8 collection campaigns</td>
</tr>
</tbody>
</table>
In this context, *L. latifolium* seems characteristic of drought-adapted, herbaceous, weedy annual plants. The high $V_{c,\text{max}}$ and $A_c-A_j$ transition CO$_2$ concentration values demonstrate the capacity of *L. latifolium* to respond to increased CO$_2$ levels. This characteristic has implications given projected increases in atmospheric CO$_2$ (Sage et al., 2008) and in demonstrating the overall robustness of the plant’s photosynthetic machinery despite high air temperatures, saline soil conditions, and warm, dry ground surface conditions. The general importance of understanding how plants respond to increases in CO$_2$ while accounting for other environmental factors is reviewed in Ainsworth et al. (2008)’s call for a new generation of elevated CO$_2$ crop experiments. The conclusions drawn from this leaf chamber study would be more robust given in tandem with free air CO$_2$ enrichment (FACE) studies, which could start to account for various adaptations and environmental interactions. There should be some caution in deriving ecological and evolutionary conclusions from leaf chamber results, as researchers (Ward and Kelly, 2004) have demonstrated that influences besides increased CO$_2$ may limit further productivity, or may drive second-generation selection towards some other characteristic (such as increased plant height or shifts in above- and belowground biomass allocation).

The results from the light curve analysis suggest a plant adjusted to high light conditions in terms of its ever-increasing ability to respond to increases in light. Even at light levels of 3000 $\mu$mol quanta m$^{-2}$ s$^{-1}$, the pepperweed leaves photosynthesize at a mean of 75% of the asymptotic value of photosynthesis ($A_{\text{max}}$). Additionally, the higher light compensation point of the two measured rosette leaves are characteristic of sun-adapted leaves (Bazzaz, 1979; Boardman, 1977). The quantum yield values (mean of 0.036) are lower than the median plant values reviewed by Skillman (2008). Drought-induced reductions in leaf water potential may also reduce quantum yield, a change attributed to chloroplast-oriented changes to the photosynthetic machinery, and not to stomatal controls (Mohanty and Boyer, 1976). It is possible that the wide range of light levels, and higher sun exposure, to which pepperweed is suited may be a trade-off from its need to capture light quickly at lower light levels. It is also possible that the numerical model used here to determine quantum yield, with its removal of very low light levels due to the Kok effect, would generate estimates lower than those determined elsewhere, a suggestion verified in an assessment of quantum yield variability by Singsaas et al. (2001).

The results presented here should provide a valuable point of comparison to ecologists and land managers interested in the spread of *L. latifolium*. Researchers have shown that some invasive species are more responsive to elevated CO$_2$ concentrations than indigenous co-occurring species (Song et al., 2009). Similarly, McDowell (2002) found that invasive species of *Rubus* (Rosaceae) have higher photosynthetic capacity, achieved at lower resources investments than the noninvasive *Rubus* species to which they were compared. Studies comparing leaf growth and net CO$_2$ assimilation between exotic and native species in Hawaii show similar findings (Baruch and Goldstein, 1999; Durand and Goldstein, 2001; Pattison et al., 1998).

On the other hand, Nagel and Griffin (2004) find minimal differences in the gas exchange parameters between the invasive *Lythrum salicaria* (purple loosestrife) and two co-occurring native species (*Asclepias syriaca*, or common milkweed, and *Solidago graminifolia*, or lance-leaved goldenrod). Similarly, Schierenbeck and Marshall (1993) find minimal differences in photosynthetic parameters between invasive *Lonicera japonica* and native *L. sempervirens*, though recognize that the higher water use efficiency and longer leaf-retention of *L. japonica* give it a competitive advantage. Owens (1996) finds that the native *Quercus virginiana* has
higher leaf gas exchange rates than its successful invader, *Juniperus ashei*, but analyzes leaf area distributions in order to demonstrate the improved competitive potential of *J. ashei*. These findings highlight the importance of canopy-level gas exchange modeling in comparing native and invasive species, rather than relying solely on leaf-level characteristics.

The leaf nitrogen-leaf mass area findings are consistent with work in many invaded ecosystems, where the exotic species has high photosynthetic capacity and the facility to access relatively large amounts of nitrogen (Rout and Callaway, 2009). Higher leaf nitrogen levels have been found in other weeds to help control photosynthetic and morphological responses to light (Mahoney and Swanton, 2008). Blank (2002) showed that pepperweed is capable of greater N-mineralization than the species it replaced (*Elytrigia elongata*, tall wheatgrass) in a study in the Honey Lake Wildlife Refuge of northeastern California. Pepperweed was capable of reaching deeper sources of nitrogen (to 50-86 cm) and can facilitate greater quantities of soil enzymes that may assist in N mineralization. The study also revealed that pepperweed “consistently produces far more biomass per unit area than vegetation it is replacing”. Blank’s work shows N content of live pepperweed leaf tissue to be 0.612%, which is similar to the average live pepperweed leaf tissue content of our study (mean 0.674%, std. dev. 0.172%, n=88).

2.5.2 Estimation Uncertainties

Estimating leaf gas exchange parameters from field measurements is full of uncertainties deriving from numerical, measurement, and sampling errors, and suffers from equifinality in that multiple parameter combinations can fit curves equally well. Some of these uncertainties have been explored in the figures presenting the sensitivity of modeled parameters on various assumptions: initial numerical conditions, differences in modeling objective functions, and differing fitting strategies. Exposing the leaf to conditions well outside its natural range creates uncertainties in time towards equilibration and the overall stationarity of parameters across these different conditions.

Estimates of $R_d$ seem especially sensitive to measurement errors and fitting methodologies because a slight change in slope can have a comparatively larger effect on the intercept. An alternative strategy for $A-C_i$ curve analysis may be to assume a temperature dependence of the variables from some initial parameterization, and then constrain the parameter estimates to fit within that range. Another alternative to using any of the methods used in this survey is to use the respiration in the dark as a direct proxy for respiration in the light, as per Flexas et al. (2007), who follow Pinelli and Loreto (2003). As Flexas et al. (2007) indicate, finding accurate estimates of $R_{light}$ is difficult because they are especially sensitive to leaks, and even to leak correction algorithms. Leak effects and the inconstancy of $\tau$ also limit the effectiveness of the Laisk method, as described in Galmes et al. (2006).

Estimates of $I^*$ using the Laisk method require careful supervision of the numerical optimization scheme if such results are to be trusted. The work presented here suggests and then rejects an approach that uses a non-rectangular hyperbola to fit the data. This fitting methodology may be more successful given a fuller dataset with more points in the range of $C_i$ values of interest: more points are needed to constrain the much greater number of parameters needed to fit this model. That is, fitting the non-rectangular hyperbola requires four parameters, whereas the linear fit requires just two. Because of state-switching, dependence on initial conditions, and local optima, a denser dataset is required if this method is to be fruitful. Such a strong dataset may however create difficulties in the field, since the leaf would be under
changing conditions for a longer period of time, so may be increasingly stressed or otherwise out of equilibrium.

Similar pitfalls deter strong conclusions regarding internal conductance. The constant $J$ and variable $J$ models of internal conductance depend on input parameters that are themselves the products of other models. The changes in curvature that $g_i$ may bring to the Laisk or $A-C_i$ datasets are not necessarily ample enough to create significant changes in an objective function based on errors in reproducing photosynthesis (Pons et al., 2009). While in some respects it seems reasonable to believe that a fast-growing, drought-tolerant species would not be limited by internal resistances to CO$_2$ diffusion, it seems equally possible that measurements presented here are not sensitive enough to conclusively state such an inference. Additional work to constrain this result could be performed, whether through measuring the variable $J$ method under lower CO$_2$ conditions or by performing isotopic fractionation analysis; both ideas are suggested by Warren (2006).

An attempt (not shown) to further constrain the parameter set by applying artificial neural network analysis to the data collected demonstrated the wide range of unpredictable variation between measurement points. A neural network analysis, like a multiple regression analysis, requires an extensive dataset, and lacks the ability to define physical process-oriented relationships. Attempting to elucidate or clarify key relationships between input and output parameters in any predictive sense using such an analysis was unsuccessful based on the survey of data collected here. A future collection of data may be more susceptible to this type of analysis given more carefully controlled input conditions (or less natural variability). Such results may be of use to other researchers to provide some estimation of confidence on parameters estimates and may also allow parameters to be derived under environmental (and not measurement) conditions.

There is additional uncertainty in the role of drought and salinity in stressing or changing leaf processes. Possible implications of soil salinity on leaf physiological processes include its effect on maintenance respiration. This portion of respiratory activity, distinct from growth-oriented respiration, includes the release of CO$_2$ to generate energy used for resynthesizing metabolites, maintaining ion gradients, and adaptation to a changing or a harsh environment (Amthor, 1984). Concurrent with environmental stresses, changing CO$_2$ conditions can change respiratory activity in a variety of possibly interactive processes (Amthor, 1991), or can increase RuBP limits to assimilation (Bongi and Loreto, 1989). Determining the functional relationships of how salinity or drought stresses may change the response of pepperweed are better suited to a more controlled study, either taking advantage of natural salinity or soil saturation gradients, or in a laboratory, greenhouse, or irrigation study. The parameters determined in this study are important reflections of the field site, and as such offer an encouraging starting point for analysis. Once they are used, in the next chapter, to evaluate a biometeorologically-based soil-vegetation-atmosphere transfer model, some plant responses to drought and salinity can be estimated through numerical modeling.
2.6 Works Cited


Chapter 3: Soil-vegetation-atmosphere transfer modeling for saline soils

3.1 Introduction: Relevance and Impact
A recent cross-disciplinary study on the global consequences of land use reports that agricultural land (including cropland and pastures) covers 40% of the earth’s surface, similar in extent to forests (Foley et al., 2005). While agricultural techniques have greatly increased food production, significant environmental damage, degraded water quality, and saline fields have been a widespread consequence of this productivity. Irrigation water often contains trace amounts of minerals that accumulate at the soil surface when the water evaporates, a process that has led to widespread abandonment of farmland in arid regions. Poor drainage can compound the problem by increasing the weathering rates of soils, which dissolve their salts into the water. Finally, the infiltration of water through saline soils enhances the suspension of soil clay particles, which then swell, disperse in the soil solution, clog soil pores and reduce the pore diameter size. This process increases the likelihood of waterlogged soils, which encourages even more soil degradation (Chapin et al., 2002; Sparks, 2003; Sposito, 1989). Hydrological behavior and soil salinity are intricately linked in many agricultural environments, where irrigation water can unintentionally produce a waterlogged sub-surface and a salt-encrusted surface layer. A crucial driver of field-level hydrology is the role of evapotranspiration, or the upward flux of water through the surface to the atmosphere. Models of plant responses to salinity in agricultural regions, then, are important tools for explaining and predicting agricultural, ecological, and atmospheric processes.

The aim of this chapter is to present and evaluate a process-based model that aggregates root, plant, and atmospheric interactions to create estimates of carbon, water, and energy fluxes at the scale of the eddy covariance tower, i.e., a field-scale fetch of approximately 500 m. This chapter builds on the previous by using the gas exchange parameters (e.g., maximum rate of carboxylation $V_{c,max}$, and the parameters governing the response of stomatal conductance to humidity) estimated at the leaf scale, and estimates how leaf and plant-level processes govern field-scale gas fluxes. In this chapter I will develop, parameterize, and test a model designed to answer the following questions:

1) How do changes in salinity influence plant behavior (e.g., how do plant stomata respond to increases in salinity)?

2) How well does a soil-vegetation-atmosphere water transfer model that incorporates salinity predict water, energy, and carbon fluxes?

Soil salinity has many implications for plant water use and growth, from increasing the soil’s osmotic pressure to toxic biochemical effects that stunt root growth and change leaf behavior. In this chapter I describe and evaluate a soil-vegetation-atmosphere water transfer model that enables a mechanistic understanding of the interplay between soil salinity, transpiration, and photosynthesis by focusing on the osmotic effects of soil salinity.

In the past, these types of vegetation stress models have been based on empirical seasonally-based yield response curves to salinity levels (Shani et al., 2007). The existing set of models often seems insufficient to capture concurrent changes in salt levels (from seasonal variations in the estuary’s fresh-salt water mix) and changes in plant behavior (from the annual solar cycle, plant phenological changes, etc.). Rather, the model validated in this study will provide a non-steady-state, physiologically-responsive, and process-based approach to salinity modeling. As a result, the patterns, mechanisms, and changes described in modeling and explaining the processes on Sherman Island will have applications to explaining other salt-
influenced vegetations, all of which can benefit from increases in temporal resolution and mechanistic understanding. For instance, crop environments still have seasonal variability in salt due to irrigation scheduling and radiation-induced surface evaporation (and so increased salinization). As water management decisions need great temporal precision, due to calls for increased efficiency and simultaneous increases in climatic uncertainty, more complex models of plant water use are necessary. This model will allow an investigation of the implications of a range of parameters and environmental conditions on the diurnal behavior of a plant or landscape. These time scales are important in determining sub-seasonal changes in CO$_2$ and H$_2$O fluxes (Valentini et al., 1995).

This work will provide benefits to the land and water management community in California by focusing on the common invasive exotic plant pepperweed (*Lepidium latifolium*). This plant is the dominant ground cover species at the research site, and is an increasing nuisance in the western United States, where it flourishes in lowland and riparian ecosystems (Chen et al., 2002). The populations of this perennial plant form dense monocultures that are spread through both clonal growth from their large rootstocks and through prolific seed production. This work will allow for models of pepperweed’s ecosystem role to be better parameterized and is based on the detailed examination of pepperweed’s photosynthesis cycle presented in Chapter 2 of this dissertation. The model will suggest pepperweed’s response to changes in environmental conditions such as light, energy, temperature, soil moisture and soil salinity. Quantifying the role of an invasive species on CO$_2$ and H$_2$O vapor exchanges is important in determining land and water use and management strategies. Invasive species have a history of changing these fluxes, with implications for landscape water use efficiency and carbon storage (Potts et al., 2008).

This chapter is organized as follows: First, soil-vegetation-atmosphere transfer SVAT models are introduced with an eye towards methods of incorporating and connecting representations of soil salinity into these depictions of water transfer (through plant transpiration) and carbon flux (through photosynthesis and respiration). Second, data collection methods used to parameterize and evaluate the model are described. This section includes descriptions of leaf-level, plant-level, and field-level data efforts. Third, the model is tested through comparison to flux estimates of a peatlands pasture site in California’s Sacramento-San Joaquin River Delta whose dominant species is an invasive herbaceous weed (*Lepidium latifolium*, called pepperweed hereafter). Finally, the implications of this modeling effort at this site are described with the goal of providing insight towards the research questions written above.

### 3.2 Introduction to soil-vegetation-atmosphere transfer modeling

#### 3.2.1. Modeling approaches

Models that represent the transfer of water from the soil through vegetation to the atmosphere are often called SVAT models. They tend to combine several approaches to study from a coherent perspective the movement of water vapor and carbon dioxide to/from the plant canopy from/to the atmosphere. The first method is to take the water flux approach, where water moves to progressively more negative pressures, guided by a series of conductances from the soil, to the root, and then through the plant and its leaves to the atmosphere. The second method looks at atmospheric drivers of evapotranspiration such as the vapor pressure deficit and solar radiation and incorporates leaf-level controls over transpiration. These two modeling approaches are often combined by solving for the leaf pressure value that allows the demand for water from the atmosphere to equal the pull of water from the plant’s root-zone.
By quantifying and comparing the effects of osmotic pressure on the Penman-Monteith-derived transpiration, researchers can see which physical relations are changed the most by adding representations of osmotic pressure and other components of salinity stress. Resolving where the effects of salinity are most seen will help assist in determining where to explore other feedback and feed-forward effects of added salinity at shorter time-scales than current models tend to explore. Recent modeling work has already shown the importance of moving from steady-state approaches to transient-state models on water resources applications of irrigation under saline conditions. For instance, Letey and Feng (2007) find that lower water applications are prescribed for equal relative yields in corn with transient-state, empirically based salinity models compared to results from steady-state analyses. Since our model incorporates both a dynamic approach (by representing hourly changes in meteorological and soil conditions) and the pseudo-instantaneous photosynthetic relationships, it can even more accurately prescribe plant water use and growth over a range of environmental conditions.

Developing schemes that scale rates of photosynthesis from the leaf to canopy level builds upon a long history of models that couple photosynthesis, stomatal conductance, and transpiration from the leaf to canopy level (Amthor, 1994; Baldocchi and Harley, 1995; de Pury and Farquhar, 1997; Harley and Baldocchi, 1995). These approaches are reviewed in Katul et al. (2000), and have been applied in agricultural environments as well as natural systems (Jones and Tardieu, 1998). Alternative strategies include model inversion to generate the leaf-scale parameters from gas exchange and energy flux data (Wolf et al., 2006; Wu et al., 2009). Ecosystem modelers relying on eddy covariance data for evaluation must take care to account for model equifinality, insensitivity to scales outside annual and diurnal drivers, and uncertainty due to parameters, model structure, and data (Medlyn et al., 2005). The model presented here builds on this history and attempts to merge it with current understandings of how to represent the role of salinity on plant processes.

### 3.2.2 Modeling Salinity

The effects of soil salinity on plants and crops has been modeled and reviewed in many previous works (Castrignano et al., 2002; Homae et al., 2002; Shani et al., 2005). Shani & Dudley (1996) describe Type I and Type II models for root water uptake under water and salt stress, and propose a Type III model combined of the other two. Type I models assume a Darcy-type flux of water to the plant root, where the driving gradient is the difference between the water potential of the root and the soil. This model commonly assumes that the plant’s response to soil matric stresses and osmotic stresses are additive, as in equation [1]:

\[
S(z, t) = K(\theta) \rho_r(D_s, t) \cdot [H_r - h(D_s, t) - \sigma_\pi \pi_{oh}(D_s, t)]  \tag{1}
\]

Where \( S(z, t) \) is the extraction of water at soil depth \( D_s \) and time \( t \), \( \theta \) is volumetric water content, \( K(\theta) \) is hydraulic conductivity of the soil, \( h \) is the matric head [m], \( \pi_{oh} \) is the soil solution osmotic head [m], and \( \rho_r \) is the root density coefficient, as in Feddes et al. (1974). A list of all parameters and their abbreviations, units, dimensions, and default values, is provided in Appendix D. The effective root water head at the soil surface \( H_r \) [m] is bound by the permanent wilting point and potential transpiration. Note that this formulation is very similar to an Ohm’s Law relationship, in which the hydraulic conductivity is replaced with a denominator of summed resistances. The term \( \sigma_\pi \) is the reflection coefficient described in Groenevelt et al. (2004), and when set to 1 gives a “minimum water availability” with respect to the salinity. This coefficient can change over time and in response to the soil’s matric and osmotic heads, and also according
to the plant species’ ability to ‘osmo-regulate’ in response to these drivers. In this work, we assume that $\sigma_r$ is equal to 1, though this assumption could change following initial modeling studies and validation efforts. Osmotic head is related to the soil solution’s electrical conductivity with the formula (Richards, 1953):

$$\pi_o = 36EC_s$$  \[2\]

where $\pi_o$ is similar to $\pi_{oh}$ but is in units of kPa and $EC_s$ is in units of dS m$^{-1}$. The solution EC, which is equivalent to the electrical conductivity of pore water removed from a saturated paste, is derived using the measured volumetric water content and the soil’s (pre-determined) porosity (Groenevelt et al., 2004) and is derived in Appendix B.

Type II models, on the other hand, assume that osmotic and water stresses reduce water uptake from a maximum value derived from Penman-Montieth-type potential evapotranspiration equations. Functionally, these stresses provoke either a threshold-linear response or an $S$-shaped response curve that is multiplicative to the maximum transpiration $S_{pot}$ (Bauer-Gottwein et al., 2008; Homaeef et al., 2002; Shani et al., 2007; Simunek et al., 2005). One such function is given here, where $\pi_{o,50}$ is the osmotic potential that causes a 50% reduction from potential extraction $S_{pot}$, and $p_\pi$ is an empirical plant parameter often set equal to 3.

$$S(D_s, t) = S_{pot}(D_s, t) \left(1 + \left(\frac{\pi_o}{\pi_{o,50}}\right)^{p_\pi}\right)^{-1}$$  \[3\]

Similar versions of this type of model also include the matric head, either additively or multiplicatively to the osmotic head, and are reviewed in Homaeef et al. (2002), and may be more amenable to replicating the toxicity effects of salinity.

Care must be taken with halophytes, or salt-tolerant species, which can use salt’s ions to their advantage in maintaining leaf turgor (Munns, 2007). For instance, Dodd and Donovan (1999) compare the osmotic and ionic effects of salty soils on both halophytes and glycophytes (which are less tolerant to soil salinity). The halophyte, *Sarcobatus vermiculatus*, had higher germination rates at more negative substrate osmotic potentials, and actually improved its fitness when NaCl was used as osmotic substrate, rather than the inert osmotant polyethylene glycol (PEG). The glycophyte, *Chrysothamnus nauseosus*, suffered in germination and seedling growth rate due to osmotic pressures but not due to ionic toxicity.

The linearity of the yield-transpiration relationship is often assumed for simplifying plant responses to drought or salinity stress, though different studies refer to economic yield or total biomass changes. These models are often based on applying a salinity factor to a crop coefficient-based empirical model of evapotranspiration (Sepaskhah et al., 2006). The temporal robustness of such an assumption was tested and supported on measurements made on tomatoes over short (weekly) time scales (Ben-Gal et al., 2003), provided that different phenological stages on seasonal timescales are accounted for. These authors establish that yield-transpiration relationships can hold for plants such as the tomato, but do not investigate sub-weekly or diurnal changes in water-use efficiency, or separate the role that soil osmotic stresses may play in governing these responses.

Incorporating the salinity models into a SVAT model that includes atmospheric drivers and leaf physiology is relatively new. To my knowledge, only Karlberg et al. (2006) have created a similar model previously, though a similar approach is used in Dalton et al. (2001), which focuses on salt accumulation in plant tissues. Our models differ in the treatment of salinity as an osmotic potential (this study) having physical effects on water uptake versus a source of stress.
derived using an empirical stress function (their studies) affecting either plant respiratory processes or water uptake. This study’s use of the Type I approach incorporated into a current-generation SVAT model is unique. The following sections develop my version of this SVAT model, whose implementation steps are then summarized (Table 3-1).

3.2.2 Soil water transport model
The water flux through the ground from the roots to the leaves is modeled as a series of conductances from the ground upwards, from the soil to the root, and then through the plant to the atmosphere. The overall soil-root-plant conductance $g_{srp}$ is used in the Darcian flow model for the flux of water ($E_{\text{Type I}}$) from the roots to the leaves, driven by the difference in pressure terms $\psi$:

$$E_{\text{Type I}} = g_{srp}[(\psi_s + \psi_o) - \psi_l]$$  \hspace{1cm} [4]

Where $\psi_l$ is the leaf water potential [MPa] driving flow from the soil, which contains two constituent water potentials: $\psi_o$, the osmotic potential [MPa], and $\psi_s$, the soil matric potential [MPa]. Here, $\psi_s$ is the soil water potential is modeled using the familiar Clapp-Hornberger relationship (1978): $\psi_s = \psi_{sat} s^{-b}$, where $\psi_{sat}$ is the soil water potential at saturation [MPa], and $b$ is a fitting parameter, and $s$ is the soil saturation percentage. Similarly, the soil’s hydraulic conductivity $K$ is modeled using Clapp-Hornberger’s relationship: $K = K_s s^{2b+3}$, where $K_s$ is the saturated hydraulic conductivity [cm day$^{-1}$]. This model assumes that the chief influence of soil salinity on water movement is through the increase in osmotic pressure, which is additive to soil potential. The components of $g_{srp}$, plant conductance $g_p$ and soil-root conductance $g_{sr}$ are now explained.

The plant conductance model reflects the stem’s reduced ability to move water when low water potentials cause air pockets to form in the plant’s xylem, a process known as cavitation (Hacke and Sperry, 2001). Under conditions where boundary layer conductance is high relative to stomatal conductance, changes in plant hydraulic conductance can linearly influence photosynthesis and stomatal conductance (Hubbard et al., 2001). The plant conductance $g_p$ in terms of unit leaf is modeled as an S-shaped function of leaf water potential (Tyree and Sperry, 1989), though exponential models can be used (Iovi et al., 2009). The Weibull function is commonly employed for this purpose (Daly et al., 2004; Sperry et al., 1998):

$$g_p = g_{pmax} \exp \left[ - \left( \frac{\psi_l}{d} \right)^c \right]$$  \hspace{1cm} [5]

where $c$ and $d$ are empirical constants here set equal to 3.85 and 3.96 MPa, respectively, based on initial calibration efforts. The maximum plant conductance, $g_{pmax}$, is assumed to be 0.082 $\mu$m MPa$^{-1}$ s$^{-1}$, based on measurements of midday-predawn leaf water potential and maximal daily evaporation (see also Figure 3-7 below). Values of $c$ were found in Sperry et al. (1998) to range between 2.64 and 9.53, and values of $d$ to range between 1.28 and 10.5 MPa. The higher $d$ values, indicating greater cavitation resistance, are for the flowering shrubs hoary leaf ceanothus (*Ceanothus crassifolius*) and mountain sagebrush (*Artemisia tridentata* ssp. *vaseyana*), and lower values for tree species box elder (*Acer negundo*) and water birch (*Betula occidentalis*). The S-shaped response used here accounts for the relatively extreme cases with acute reductions in plant conductance or leaf-stem homeostasis. Seasonal shifts in vulnerability to cavitation (Jacobsen et al., 2007) and the metabolic signaling processes that govern xylem responses to drought (Alvarez et al., 2008) are not considered here. Water storage or hydraulic capacitance is
also not incorporated, as its importance is greater in trees than in small plants (Carlson and Lynn, 1991; Lhomme et al., 2001).

There are many ways to model the movement of water in the root-zone towards the plant (Wang and Smith, 2004). I choose a relatively simple model governed primarily by the soil’s hydraulic conductivity to represent the soil-root conductance $g_{sr}$ per unit ground area, per Katul et al. (2003) and Daly et al. (2004):

$$g_{sr} = \frac{K\sqrt{R_{AI}}}{\pi g \rho w Z_r} \quad [6]$$

which assumes a simplified cylindrical root model, and where $K$ is the Clapp-Hornberger hydraulic conductivity, $R_{AI}$ is the corrected root area index, $\rho_w$ is the water density, and $Z_r$ is the root depth. The root index $R_{AI}^*$ is corrected for the compensation of the plant to low water conditions using the following relation: $R_{AI}^* = R_{AI}^{c^{-a}}$, where $a$ is taken as 8. $R_{AI}^*$ is assumed to scale with leaf area index $L_{AI}$ such that $R_{AI}^* = 4L_{AI}$. This type of root compensation is similar to the work of Guswa et al. (2004) and Guswa (2005), which shows that one-bucket models are sufficient to capture plant behavior if a root fraction term is included.

The root distribution in the soil profile is non-uniform, and so should be considered in weighting regions of different soil moisture. In this model the logistic dose-response curve suggested in Schenk and Jackson (2002) is used with best-guess parameters for Lepidium latifolium:

$$r_{frac}(D_z) = \left[1 + \left(\frac{D_z}{D_{50}}\right)^c\right]^{-1} \quad [7]$$

In this equation $r_{frac}(D_z)$ is the cumulative amount of roots higher than profile depth $D_z$ (in cm), $D_{50}$ is the depth in cm where $r_{frac}(D_z)$ is 0.5, and $c$ is a shape parameter. Schenk and Jackson (2002) provide estimates of these parameters for a global dataset grouped by vegetation type, and suggest values in deserts and semi-desert shrublands of 27 cm for $D_{50}$ and -1.91 to -2.05 for $c$. For L.latifolium, Renz and Blank (2004) state that in a riparian habitat, 19% of the below ground biomass is present in the top 10 cm of soil, with 85% in the top 60 cm. The near-surface biomass largely consists of a semiwoody crown from which the shoots emerge. Roots have been known to penetrate deeper than 3 m, and can penetrate to the fringes of the water table. Some evidence of metabolic adaptation to anaerobic soil conditions has been discovered (Chen and Qualls, 2003). Because of the semiwoody nature of the near surface root portion and its ability to reach the water table, it seems reasonable to infer that most water-generating portions of the root structure occur below this region and just in and above the water table. Therefore, in this study, I suggest parameterizing the model in equation [7] with parameter values -2 for $c$, and 50 cm for $D_{50}$, for the purpose of finding the root-weighted average soil moisture. Soil moisture saturation and pore electrical conductivity through the soil profile are interpolated from probe-based measurements, and then mean values are derived through arithmetic weighting across the soil profile in proportion with the root fractioning.

Future models in saline soil environments could consider the effects of salinity on root hydraulic conductivity if they can be separated from other salinity-induced stresses. This root conductivity is an important plant property that allows water to move from the soil to the plant stem. There is some evidence that under salty soil conditions, root hydraulic conductivity, particularly for glycophytes, is reduced due to dehydration, pore blockage by solutes, and aquaporin protein expression (Azaizeh and Steudle, 1991; Carvajal et al., 1999; Martínez-
Ballesta et al., 2003; Martinez-Ballesta et al., 2000; Rodriguez et al., 1997; Ye et al., 2005), though this is not always the case (Katsuhara and Shibasaka, 2007). These effects may be more likely in less halophytic plants, and are not incorporated in the present model.

The overall soil-root-plant conductance per unit ground area is modeled to incorporate the relative importance of root and xylem conductance, depending on which one is more limiting. The overall conductance is taken as per Daly et al. (2004) and Sperry et al. (2002):

\[ g_{srp} = \frac{L_{AI}g_{sr}g_p}{g_{sr} + L_{AI}g_p} \]  \[ \text{[8]} \]

The Darcian transpiration method derived in this section is used with the Penman-Monteith approach described below to jointly resolve the system’s transpiration and leaf water potential, as in Daly et al. (2004).

### 3.2.3 Modeling Transpiration and Plant-Atmosphere Interactions

Transpiration models depend on atmospheric and energetic forcing conditions, plant-specific stomatal and physiological characteristics, and interactions with other members of the ecological landscape. These interactions are generally implemented in a Penman-Monteith (Monteith, 1965) formulation:

\[ E = \frac{\left(\Delta \phi + \rho_a D C_p g_{ba}\right) g_{sv} L_{AI}}{\rho_w \lambda_w (\Delta g_{sv} L_{AI} + \gamma (g_{ba} + g_{sv} L_{AI}))} \]  \[ \text{[9]} \]

where the atmospheric water vapor deficit is defined as \( D = e_{sat}(T_a) - e_a \), the net radiation is defined as \( \phi = R_n - G \) (where \( R_n \) is the net radiation and \( G \) is the ground heat flux), \( g_{ba} \) is the conductance series between the leaf boundary and the atmosphere, \( g_{sv} \) is the stomatal conductance of water vapor, \( \lambda_w \) is the latent heat of water vaporization, \( \gamma \) is the psychrometric constant, \( \Delta \) is the slope of the \( e_{sat}(T_a) \) relationship, \( \rho_a \) and \( \rho_w \) are the densities of air and water, respectively, and \( C_p \) is the specific heat of air. The leaf area index \( L_{AI} \) is the area of leaves per ground area, and has been found to be useful in moving from the leaf-scale to the field-scale, and is also of importance in predictive modeling of plant responses to elevated CO\(_2\) (Ewert, 2004). This scaling removes other terms composing common representations of bulk surface conductance such as cuticular and soil conductance (Baldocchi et al., 1987). Soil conductance is inversely related to near surface soil moisture (Camillo and Gurney, 1986), which is often very low (VWC<0.05% at 2 cm) at the field site. Cuticular conductance is often a small portion of stomatal conductance (Boyer et al., 1997), and so is ignored. When the model is run with a partition between sunlit and shaded leaf area, the sum of the Penman-Monteith estimates from these canopy areas is used to equal the water flux transpiration using the Type I method above.

Most relevant for the discussion of the interactions of salinity and soil water stresses is the stomatal conductance term (or its inverse, stomatal resistance). Stomata are valves in all plant surfaces that control transpiration, or the release of water vapor into the atmosphere. While there are many controls on plant stomata (Hetherington and Woodward, 2003), this work focuses on environmental influences on stomatal activity. Many stomatal models consider mechanistically the dependence of stomatal conductance on net carbon assimilation and atmospheric carbon dioxide concentrations (Ball et al., 1987; Collatz et al., 1991; Katul et al., 2000; Leuning, 1995). Typically, the Jarvis model (1976) does not include a description of stomatal closure under drying soil conditions; nor does it include the effects of soil salinity. The first set of models are collectively called “Ball-Berry”-type models, and require a model of
photosynthesis (or net assimilation, $A_n$). In this chapter I use the Ball-Berry model of Leuning (1995), as adjusted by others (Dewar, 2002; Tuzet et al., 2003), who use internal CO$_2$ concentration $c_i$ in place of the leaf surface CO$_2$ concentration $c_s$. This adjustment accounts for observations (Mott, 1988) that stoma respond to the substomal concentration that drives photosynthesis. This adjusted equation is:

$$g_{s,CO_2} = \frac{a_1 A_n f_D(D)}{c_s - \Gamma^*}$$ \[10\]

This model assumes a negligible residual conductance (i.e., from the plant cuticles). The parameters $a_1$ and $f^*$ represent the linear dependence of $g_s$ on net assimilation and the photorespiration point, respectively. While $a_1$ is parameterized in Chapter 2 as 11.25 for the stomatal conductance of CO$_2$, it is taken as 16.9 in this chapter because of an addition (below) to this equation that accounts for reductions due to low leaf pressure. The function $f_D(D)$ represents the reduction to stomatal conductance under atmospheric water vapor deficits as plants fight to conserve loss of water per carbon intake, and this is modeled relative to a reference deficit $D_x$:

$$f_D(D) = \frac{1}{1 + D/D_x}$$ \[11\]

In Chapter 2 of this dissertation a value of 1.0 kPa for $D_x$ is determined by best fit to leaf data, and Leuning (1995) suggests a value of 1.25 kPa. Initial calibration work here suggests a value of 1.50 kPa, and the $D_x$ value will be investigated in further detail in the following chapter’s sensitivity analysis.

Diffusion of CO$_2$ from the leaf surface to interior is governed by stomatal conductance, so that it may also be defined as:

$$A_n = g_{s,CO_2}(c_s - c_i)$$ \[12\]

Where $c_i$ is the concentration of CO$_2$ inside the stomata. Similarly, the diffusion of CO$_2$ from the open atmosphere depends on the combined series of CO$_2$ atmospheric, leaf boundary layer, and stomatal conductance:

$$A_n = g_{sba,CO_2}(c_a - c_i)$$ \[13\]

Where $c_a$ is the atmospheric concentration of CO$_2$. It is assumed that the stomatal conductance of water is related to the stomatal conductance of CO$_2$ by accounting for the different gas diffusivities:

$$g_{sv} = 1.6g_{s,CO_2}$$ \[14\]

The CO$_2$ balance inside the stomatal pores is described by the steady-state condition:

$$A_n = A - P_n - R_d$$ \[15\]

While daytime respiration $R_d$ is neglected for simplicity in other SVAT models (Daly et al., 2004; Dewar, 1995; Katul et al., 2003), or is parameterized as a fraction of carboxylation potential $V_{c,max}$ (Collatz et al., 1991), it is included here based on its temperature-dependent parameterization in Chapter 2. Photorespiration $P_n$ and carboxylation $A$ are modeled as dependant on $\phi$, $c_i$, $\psi_l$, and leaf temperature $T_l$; effects of nutrient status and internal oxygen concentration are ignored. The reduction of $A_n$ in water-stressed conditions follows Daly et al. (2004), where there are reductions from a well-watered potential photosynthesis (or stomatal conductance) based on a function $A_{\psi_l}(\psi_l)$:

$$A_n = A - P_n - R_d = A_{\psi_l}(\psi_l) \times A_{\phi,c_i,T_l}(\phi, c_i, T_l) - R_d$$ \[16\]
The $A_{\psi_l}(\psi_l)$ model simulates the reduced net photosynthetic capacity of stressed leaves with more negative values of leaf water potential, where cellular dehydration drives reductions in ATP availability that lower RuBP regeneration (Tezara et al., 1999). Past models of C$_3$ plants in semiarid ecosystems (Daly et al., 2004; Friend, 1995) use a linear response to leaf water potential, but in this model I have implemented the empirical logistic response function used in Tuzet et al. (2003) and Siqueira et al. (2008) to depict the reduction to stomatal conductance at more negative leaf water potentials:

$$A_{\psi_l}(\psi_l) = \frac{1 + \exp(s_f\psi_l)}{1 + \exp(s_f(\psi_f - \psi_l))} \quad [17]$$

where $s_f$ and $\psi_f$ are parameters that depend on morphological adaptations in different species, and are adjusted in the model development process to reflect the response of pepperweed to leaf water potentials. Where Tuzet et al. (2003) use this function in place of equation [11], I suggest following Daly et al. (2004) in including separately the responses of stomata to both vapor pressure deficit and to leaf water potential. Thus the stomatal conductance model allows for the distinct but related contributions of $g_s$ on $\psi_l$, $D$, and CO$_2$, and so it can simulate in part measured increases in the stomatal conductance of leaves under highly negative water potentials to lowered CO$_2$ concentrations even under high vapor pressure deficits (Bunce, 2006; Bunce, 2007). The addition of this function may force the $a_l$ slope parameter to be higher to compensate for possible reductions due to low leaf water potential. This hypothesis will be examined in more detail in Chapter 4 of this dissertation.

The rate of net photosynthesis is also a function of the leaf’s potential capacity to fix carbon, which is a relationship between $A_c$, the assimilation rate limited by rubisco activity (i.e., under low CO$_2$ concentrations, and so dependent on $c_i$), $A_q$, the assimilation rate limited by RuBP regeneration when low light availability limits the photosynthetic electron transport rate, and $A_s$, the assimilation rate under high $c_i$ and $\phi$ but limited by leaf temperature. This relationship will be explained in more detail below.

Following Daly et al. (2004), the stomatal function then becomes:

$$g_{s,CO_2} = a_1A_{\psi_l} \times A_{\phi,c_i,T_l}(\phi, c_i, T_l) \frac{f_D(D)}{c_s - \Gamma^*} \quad [18]$$

The assimilation model used is based on Farquhar et al. (1980) and its followers. It is taken from Daly et al. (2004), and ignores the role of mesophyll conductance. The rubisco-limited rate of photosynthesis is:

$$A_c = \frac{V_{c,max}(c_i - \Gamma^*)}{c_i + K_c \left(1 + \frac{c_i}{K_2}\right)} \quad [19]$$

Where $K_c$ and $K_o$ are the Michaelis-Menten coefficients for CO$_2$ and O$_2$, respectively, $\Gamma^*$ is the photo-compensation point, $V_{c,max}$ is the maximum rate of carboxylation, and $o_i$ is the oxygen concentration, assumed constant. The light-limited rate of photosynthesis is taken as:

$$A_q = \frac{J(c_i - \Gamma^*)}{4(c_i + 2\Gamma^*)} \quad [20]$$

where $J$ is the electron transport rate when the absorbed photon irradiance is $Q$, and is given by the lower root of the equation:
\[
\kappa_1 J^2 - (\kappa_2 Q + J_{\text{max}})J + \kappa_2 Q J_{\text{max}} = 0
\]  \quad [21]

where, by Leuning (1995), \( \kappa_1 = 0.95 \) and \( \kappa_2 = 0.20 \) mol electrons mol\(^{-1}\) photons. \( J_{\text{max}} \) is parameterized in an Arrhenius function using the dataset gathered in Chapter 2. In saturating light and carbon dioxide concentrations, assimilation reaches a maximal value \( A_s \), set as in Collatz et al. (1991):

\[
A_s = V_{c, \text{max}} / 2
\]  \quad [22]

To account for the gradual transition between these assimilation rates to get \( A_{\phi, c_i, T_i} \), Collatz et al. (1991) propose using the lower roots of the following:

\[
\beta_1 A_p^2 - (A_c + A_q)A_p + A_c A_q = 0
\]  \quad [23]

and

\[
\beta_2 A_{\phi, c_i, T_i}^2 - (A_p + A_s)A_{\phi, c_i, T_i} + A_p A_s = 0
\]  \quad [24]

Where \( A_p \) is an intermediate value that gives the minimum between \( A_c \) and \( A_q \) and \( \beta_1 \) and \( \beta_2 \) are empirical constants. The Michaelis-Menten coefficients, the maximum carboxylation rate, and the leaf temperature dependence of the CO\(_2\) carboxylation point are modeled using functions developed in Chapter 2 of this dissertation.

The canopy-scale atmospheric conductance and leaf boundary layer conductance govern the movement of scalars from the leaf to the atmosphere. The model represents aerodynamic resistance \( r_a \), governing momentum transfer between the atmospheric measurement or reference height \( z \) and the vegetation height \( z_{veg} \), according to the Monin and Obukov similarity theory to account for atmospheric stratification (Goudriaan, 1977; Wang et al., 2007). These estimates use the friction velocity \( u^* \) determined from the eddy covariance data by the method of Stull (1988):

\[
u^* = \left[ \frac{u'}{\overline{u}} \right]^2 + \left[ \frac{v'}{\overline{v}} \right]^2 + \left[ \frac{w'}{\overline{w}} \right]^2 \right]^{1/2}
\]  \quad [25]

where \( u', v', \) and \( w' \) are the wind fluctuations around the mean in the horizontal, lateral, and vertical directions, respectively. The overbar indicates a Reynolds time averaging of turbulent fluctuations over time. For stable atmospheric conditions (when Monin-Obukhov length \( L > 0 \)), the aerodynamic resistance from the middle canopy to the reference or measurement height is:

\[
x_{a, \text{st}} = \frac{u}{u^*} = \frac{0.74}{\kappa u^*} \left[ \ln \left( \frac{z - 0.5z_c}{z_{0}} \right) - \ln \left( \frac{z - z_d}{z_{0}} \right) + 4.7 \left( \frac{z - z_d}{L} \right) - 4.7 \left( \frac{z - z_d}{L} \right) \right]
\]  \quad [26]

Where \( \kappa \) is the von Kármán constant (0.41), \( z \) is the measurement height, \( z_d \) is the zero-plane displacement (set to 0.67\( z_{veg} \)), and \( z_0 \) is a roughness parameter (set to 0.1\( z_{veg} \)). Canopy height \( z_{veg} \) is allowed to scale with \( L_{AI} \) up to an upper limit of 1.5 m, such that height \( z_{veg} = \min(L_{AI}, 1.5) \), based on observations in the field. Measurement height at the site of interest is 2.5 m. The aerodynamic conductance \( g_a \) is simply \( r_a^{-1} \). Under unstable atmospheric conditions (where \( L < 0 \)), the aerodynamic resistance from mid-canopy to the reference height is:

\[
x_{a, \text{unst}} = \frac{0.74}{\kappa u^*} \ln \left( \frac{z - z_d}{z_{0}} \right) - \ln \left( \frac{z - z_d}{z_{0}} \right) - 2 \ln \left( 1 + \frac{1 - \frac{z_r - z_d}{L w}}{2} \right)
\]  \quad [26]

+ 2 \ln \left( 1 + \frac{1 - \frac{z_r - z_d}{L w}}{2} \right) + 0.37 \frac{z_c}{l_m} \exp \left( \frac{k w}{L} \right) - 1
\]  \quad [27]
Where $L_w$ is a characteristic leaf dimension (width) [m], and where $l_m$ is the mean mixing length, given as (Wang et al., 2007):

$$l_m = 1.2 \sqrt[3]{4L_w z_c / \pi / LAI}$$  \[28\]

Where $k_w$ is the extinction coefficient of wind speed by the canopy, given as (Goudriaan, 1977)

$$k_w = \left( \frac{0.15 \cdot LAI \cdot z_{veg}}{l_m} \right)^{0.5}$$  \[29\]

The leaf-boundary layer conductance model follows Nikolov et al. (1995) and others in using non-dimensional groups to quantify the interaction of the leaf and its immediate atmospheric boundary (Schuepp, 1993). The all-sided leaf-boundary layer conductance to water vapor [m s$^{-1}$] is:

$$g_{bv} = \frac{D_v S_h}{L_w}$$  \[30\]

where $L_w$ is the characteristic leaf dimension used above, which is taken as the leaf width for broad leaves or the needle diameter for conifers, $D_v$ is the molecular diffusivity of water vapor in air [m$^2$ s$^{-1}$], which is a function of absolute air temperature and barometric pressure, and $S_h$ is the Sherwood number, which is a function of other dimensionless groups (the Nusselt number, Reynolds number, and Prandtl number). This representation can be simplified under certain atmospheric conditions. In the case of forced convection and laminar air flow over the leaf surface, the forced-convective leaf boundary-layer conductance ($g_{bvf}$) can be derived as [m s$^{-1}$]:

$$g_{bvf} = c_f T_{ak}^{0.56} \left[ (T_{ak} + 120) \frac{u}{L_w P} \right]^{0.5}$$  \[31\]

where $c_f$ is a parameter that equals 4.322x10$^{-3}$ for broad leaves, $T_{ak}$ is the absolute air temperature [K], $u$ is the wind velocity [m s$^{-1}$], and $P$ is atmospheric pressure [Pa]. This forced-convective leaf boundary-layer conductance has very low temperature sensitivity, so, as per Nikolov et al. (1995), is calculated using the free-air temperature rather than the leaf surface temperature.

Heat and vapor exchange at low wind speeds are dominated by free convection, and so depend on the Grashof number, which is based on the absolute difference in virtual temperatures between the leaf surface and the ambient air. From this and other terms, the free-convective leaf boundary-layer conductance ($g_{bve}$) is derived [m s$^{-1}$]:

$$g_{bve} = c_v T_{lk}^{0.56} \left[ \frac{T_{lk} + 120}{P} \right]^{0.5} \left[ \frac{T_{vl} - T_{va}}{L_w} \right]^{0.5}$$  \[32\]

Where $c_v$ is a parameter that equals 1.6361x10$^{-3}$ for broad leaves, $T_{lk}$ is the absolute leaf temperature [K], and $T_{vl}$ and $T_{va}$ are the virtual temperatures of the leaf and free air [°C], respectively, whose difference is calculated using:

$$T_{vl} - T_{va} = \frac{T_{lk}}{1 - 0.378e_b/P} - \frac{T_{ak}}{1 - 0.378e_a/P}$$  \[33\]

where $e_b$ and $e_a$ are the water-vapor pressure [Pa] inside the leaf boundary layer and the free air, respectively. For a dry leaf, $e_b$ also depends on $e_{sat}(T_l)$, which is the saturated vapor pressure $e_{sat}$ [Pa] at the leaf temperature $T_l$ [°C]:

$$e_b = \frac{g_{sv} e_{sat}(T_l) + g_{bve} e_a}{g_{sv} + g_{bve}}$$  \[34\]
where the dependence of $e_b$ on $g_{hve}$ generates a feedback that can be solved iteratively, and in combination with an analytical solution for leaf temperature, also dependent on leaf boundary layer conductance, which is given below. The final leaf boundary-layer conductance to water vapor ($g_{bv}$) is the greater of the forced and free convective conductances. Testing the dataset from Sherman Island, California, indicated that in nearly all cases, given any reasonable input of stomatal conductance, that the forced convective conductance is greater than the free convective conductance. This result has the effect of simplifying the model’s implementation because $g_{bv}$ is a straight-forward function of wind-speed and temperature, and avoids the feedbacks in the $g_{hve}$ analysis.

The leaf energy balance is derived analytically based on the balance between energy absorbed by a leaf and its dissipation through latent and sensible heat fluxes, long-wave radiation and metabolic storage:

\[
R_i = \frac{\rho c_p}{\gamma} [e_{sat}(T_i) - e_a] g_{tv} + \rho c_p (T_i - T_a) g_{bH} + 2\varepsilon\sigma_S B (T_i + 273.16)^4 + M_e
\]  

[35]

Where $R_i$ is the bidirectional absorbed short- and long-wave radiation [W m\(^{-2}\)], $c_p$ is the specific heat of dry air (1010 J kg\(^{-1}\) K\(^{-1}\)), $\gamma$ is the psychrometric constant [Pa K\(^{-1}\)], $g_{bH}$ is the leaf boundary layer sensible heat conductance, $g_v$ is the leaf total conductance for water-vapor exchange [m s\(^{-1}\)] through the stomata and boundary layer, $T_a$ is the ambient air temperature, $\varepsilon$ is the leaf thermal emissivity (0.975), and $\sigma_{SB}$ is the Stefan-Boltzmann constant (5.6x10\(^{-8}\) W m\(^{-2}\) K\(^{-4}\)). In the model used here $R_i$ is simplified as the fraction of $\phi$, or $R_n$-$G$, assigned to that portion of the canopy (i.e., the sunlit or shaded portion). The energy stored in metabolic processes and biochemistry ($M_e$) is considered here as negligible, so is ignored, though some researchers (Meyers and Hollinger, 2004) suggest including it. The saturated water vapor pressure $e_{sat}$ increases exponentially with temperature and can be computed via approximation with a fourth-order polynomial for analytical convenience:

\[
e_{sat}(T_i) = 5.82436 \times 10^{-4} T_i^4 + 1.5842 \times 10^{-2} T_i^3 + 1.55186 T_i^2 + 44.5135967 T_i + 607.919
\]  

[36]

The polynomial version of this equation is only used to derive leaf temperature; elsewhere in this model an exponential form is used, dependent upon temperature $T$ [°C]:

\[
e_{sat}(T) = 611 \exp \left( \frac{17.3 T}{T + 237.3} \right)
\]  

[37]

The two models differ by a maximum 0.56% at -2°C (Gueymard, 1993).

The conductance terms $g_{tv}$ and $g_{bH}$ are calculated as:

\[
g_{tv} = \frac{g_{sv} g_{bv}}{g_{sv} + g_{bv}}
\]  

[38]

And

\[
g_{bH} = 0.924 g_{bv}
\]  

[39]

which holds for both free and forced convection.

The leaf energy balance is exactly solved using a quartic equation for $T_i$:

\[
T_i^4 + a_t T_i^3 + b_t T_i^2 + c_t T_i + d_t = 0
\]  

[40]

where the coefficients are:
The analytical solution to this quartic equation of temperature, as provided in Nikolov et al. (1995), is given in Appendix A.

### 3.2.4 Plant canopy model

The sun-shade model uses representations of the penetration of light through the canopy, which is a function of leaf area index and other canopy characteristics. In this study we use the “two-leaf” sun/shade model of de Pury and Farquhar (1997), which allows for calculating the absorption of the incoming stream of direct and diffuse radiation by sunlit and shaded leaves. This model is reviewed briefly here. Both de Pury and Farquhar (1997) and Dai et al. (2004) use the following method to partition the total leaf area into sunlit and shaded leaf portions ($f_{sun}$ and $f_{shade}$ respectively) at a canopy depth $x$:

\[
f_{sun}(x) = e^{-k_b x} \quad \text{and} \quad f_{shade}(x) = 1 - f_{sun}(x)
\]

Where $x$ is the cumulative leaf area index measured downwards from the top of the canopy and $k_b$ is a canopy extinction coefficient defined below. Integrating equation [45] over the leaf area $L_{AI}$ yields:

\[
L_{Sun} = \int_0^{L_{AI}} f_{Sun}(x) dx = \frac{1}{k_b} (1 - e^{-k_b L_{AI}})
\]

\[
L_{Shade} = L_{AI} - L_{Sun}
\]

Irradiance absorbed by the whole canopy $I_c$ is the sum of the irradiance absorbed by the sunlit and shade fractions of the canopy:

\[
I_c = I_{cSun} + I_{cSh}
\]

The sunlit fraction of the canopy absorbs direct-beam ($I_{lb}$), diffuse ($I_{ld}$), and scattered-beam ($I_{lbs}$) components:

\[
I_{cSun} = \int_0^{L_{AI}} I_{lsun} f_{Sun}(L) dL = \int_0^{L_{AI}} [I_{lb} + I_{ld} + I_{lbs}] f_{Sun}(L) dL
\]

The direct beam irradiance absorbed by sunlit leaves is:

\[
\int_0^{L_{AI}} I_{lb} f_{Sun}(L) dL = I_b(0)(1 - \sigma)[1 - \exp(-k_b L_{AI})]
\]

The diffuse irradiance absorbed by sunlit leaves is:
The scattered irradiance absorbed by sunlit leaves is:

\[ \int_0^{l_{AI}} l_{d} f_{Sun}(L) dL = l_d(0)(1 - \rho_{cd}) \times \{1 - \exp[-(k'_d + k_b)L_{AI}])k'_d/(k'_d + k_b) \} \]

And the scattered irradiance absorbed by sunlit leaves is:

\[ \int_0^{l_{AI}} l_{d} f_{Sun}(L) dL = l_d(0)[(1 - \rho_{cb})(1 - \exp[-(k'_b + k_b)L_{AI}])k'_b/k'_b + k_b] - (1 - \sigma)[1 - \exp(-2k_bL_{AI})]\]

The total irradiance absorbed by the canopy is given as:

\[ I_c = \int_0^{l_{AI}} l_d dL = (1 - \rho_{cb})l_b(0)[1 - \exp(-k'_bL_{AI})] + (1 - \rho_{cd})[1 - \exp(-k'_dL_{AI})] \]

And the total irradiance absorbed by the shaded part can be derived from the difference between \( I_c \) from equation [52] and \( I_{cSun} \) from equation [48] using equation [47].

The parameters of this model are taken from de Pury and Farquhar (1997): the leaf scattering coefficient of PAR \( \sigma \) is the sum of the leaf reflection coefficient for PAR \( \rho_l \) and the leaf transmissivity to PAR \( \tau_l \); these are taken as 0.15, 0.10, and 0.05, respectively. The canopy reflection coefficient for diffuse PAR \( \rho_{cd} \), is taken as 0.036 and the diffuse PAR extinction coefficient \( k_d \) is taken as 0.78. The PAR extinction coefficients for direct (\( k'_b \)) and diffuse (\( k'_d \)) light that account for scattering, are functions of beam and diffuse extinction coefficients \( k_b \) and \( k_d \), respectively, and the leaf reflection coefficient:

\[ k' = k(1 - \sigma)^{1/2} \]

The direct beam extinction coefficient \( k_b \) is derived following Sellers (1985) and Dai et al. (2004), as a function of \( \mu \), the cosine of solar zenith angle:

\[ k_b = G(\mu)/\mu \]

where the function \( G \), representing the projected area of phytoelements in the direction of the sun, is given as:

\[ G(\mu) = \phi_1 + \phi_2 \mu \]

\[ \phi_1 = 0.5 - 0.633\chi - 0.33\chi^2 \]

\[ \phi_2 = 0.877(1 - 2\phi_1) \]

where \( \chi \) represents the leaf angle distribution, and varies from -1 for vertical leaves, 0 for leaves in a spherical angle distribution, and 1 for horizontal leaves. This model is parameterized and checked against measured incoming, reflected, and diffuse PAR at the field site.

Including the distinction for sun and shade leaves in a SVAT model that considers plant hydraulics and soil characteristics assists in distinguishing this work from previous studies. For example, Tuzet et al. (2003) use a big-leaf approach to investigate the importance of water flow from the soil through the plants to the atmosphere in the context of a canopy model of CO\(_2\) exchange. Similarly, Karlberg et al. (2006) do not appear to separate the model into multiple parts in their study of the role of salinity on gas and water exchange in tomato crops. The importance of separating these portions of the canopy is verified by previous research (Reynolds et al., 1992).
3.2.5 Model algorithm

The system of equations and relationships above is implemented on a half-hourly time-step (Table 3-1), and is forced by data from the FLUXNET site, including soil moisture, incoming net radiation, atmospheric vapor pressure deficit, and atmospheric temperature. The set of equations allows the variables \( \psi_l, \psi_s, \) \( g_{sv} \) and \( E \) to be resolved for each time step. Leaf pressure is assumed to be constant throughout the plant, so whether the leaves are sunlit or shaded, they will have the same leaf pressure. This assumption is in part due to the dominance of the plant’s stem pressure in determining leaf pressure, which we assume does not vary much through the height of the plant. This assumption finds support in Ewers et al. (2007), who show that variations in stomatal conductance through the canopy are driven by differences in light penetration, but suggest that leaf pressures changes much less through the canopy.

The model algorithm finds the leaf pressure value which minimizes the difference between the atmospherically-driven transpiration (i.e., as determined through the Penman-Monteith equation) and the plant-soil transpiration (i.e., determined through the water flux method). This leaf pressure must also generate a stomatal conductance (through inversion of the Penman-Monteith equation) that allows equal photosynthesis estimates from the chemistry-based method (equation [16]) and the diffusion-based method (equation [13]). This routine accounts for the difference between sunlit and shaded leaves by also optimizing the fraction of plant transpiration (as a function of leaf pressure) that is portioned to each type of leaf; i.e.,

\[
E_{Type1} = E_{sh} + E_{sun} = (1 - f)E_{Type1} + f \cdot E_{Type1}
\]

Where \( E_{sh} \) and \( E_{sun} \) are the evapotranspiration rates from the shaded and sunlit portions of the canopy, respectively, and \( f \) is the fraction of plant transpiration assigned to the sunlit part of the canopy. These rates are moderated by separate estimates of \( g_{sv} \) for each canopy part, though they share the same leaf potential estimate (\( \psi_l \)), as explained above.

The model has governing parameters summarized in Appendix D, and the algorithm is summarized in Table 3-1. This model is evaluated with and without the osmotic potential term to test the effects of salinity. Daily and seasonal cumulative evapotranspiration and carbon uptake are compared to eddy covariance derived estimates to test model performance. Some of the parameters (e.g., \( L_{AI} \) and \( D_x \)) are studied in more detail for their role in determining model outcomes, while a more rigorous sensitivity analysis is performed in Chapter 4.
Table 3-1: Model algorithm steps, implemented half-hourly during daytime through the growing season, implemented on Matlab v7.4.0.

<table>
<thead>
<tr>
<th>Step</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Step 1: Input values, parameters</strong></td>
<td>Load measured environmental data</td>
</tr>
<tr>
<td></td>
<td>- ( u, u^*, D, PAR, PAR_d, R_n, G, T_a, \theta, EC, \rho )</td>
</tr>
<tr>
<td></td>
<td>- ( L_{sl} ) estimate</td>
</tr>
<tr>
<td></td>
<td>Establish parameter values</td>
</tr>
<tr>
<td><strong>Step 2: Calculate environmentally-determined state variables</strong></td>
<td>Determine:</td>
</tr>
<tr>
<td></td>
<td>Root distribution (Equation [7]) and weighted ( \theta )</td>
</tr>
<tr>
<td></td>
<td>Partition of the leaf canopy into shade/sun fractions, and incident light to each (Equations [45] to [55])</td>
</tr>
<tr>
<td></td>
<td>( r_s ) (Equations [26] to [29])</td>
</tr>
<tr>
<td></td>
<td>( r_b ) (Equation [31])</td>
</tr>
<tr>
<td></td>
<td>( \pi_{rs}, g_{sr} ) (Equation [2]; [6])</td>
</tr>
<tr>
<td><strong>Step 3: Establish boundary conditions</strong></td>
<td>Establish feasible bounds on ( \psi_l ) by grid search of ( \psi_l ) values, which generates</td>
</tr>
<tr>
<td></td>
<td>( g_p ) (equation [5]),</td>
</tr>
<tr>
<td></td>
<td>( g_{srp} ) (equation [8]),</td>
</tr>
<tr>
<td></td>
<td>( E ) (equation [4]), and</td>
</tr>
<tr>
<td></td>
<td>( g_{sv} ) by inverting equation [9],</td>
</tr>
<tr>
<td></td>
<td>because too-low ( \psi_l ) can generate negative or infinite ( g_{sv} )</td>
</tr>
<tr>
<td><strong>Step 4: Minimization function [fmincon]</strong></td>
<td>Find ( \psi_l, E, ) and ( f )</td>
</tr>
<tr>
<td></td>
<td>which generate the sunlit and shaded ( g_{sv} ) that minimize the difference between photosynthesis estimates from the chemistry-based method (equations [15], [16]) and the diffusion-based method (equations [12] and [13]) for each canopy half (i.e., equation [56]). Requires:</td>
</tr>
<tr>
<td></td>
<td>( A_{sl} ) (equation [17])</td>
</tr>
<tr>
<td></td>
<td>( T_i ) (equations [35]-[44]; Appendix A)</td>
</tr>
<tr>
<td></td>
<td>( A_{\phi,ci,T} ) (equations [18]-[24])</td>
</tr>
<tr>
<td><strong>Step 5: Check solution</strong></td>
<td>Verify:</td>
</tr>
<tr>
<td></td>
<td>( E ) from [4], [9], and [56] are consistent,</td>
</tr>
<tr>
<td></td>
<td>( A_n ) from [12] and [13] are consistent with ( A_n ) from [16], and</td>
</tr>
<tr>
<td></td>
<td>( T_{li} ) and ( g_{sv} ) are finite and positive</td>
</tr>
</tbody>
</table>

3.3 Validation Site and Field Methods

3.3.1 Evaluation Site Description

Model evaluation is performed using data from a peatlands pasture site on Sherman Island, in California’s San Francisco Bay-Sacramento River Delta ecosystem. This site is part of the FLUXNET project (Baldocchi et al., 2001), and is dominated by a discontinuous canopy of perennial pepperweed but also includes the nonnative annual C3 grass *Hordeum murinum*. The prime field site is an irrigated pasture over peat soils more than 7 m thick (Deverel and Rojstaczer, 1996). This site is on Sherman Island, which is on the west side of the Delta and is on land managed by the California Department of Water Resources (lat: 38.0373°N; long: 121.7536°W; Elevation -12.1 m). The site has ideal fetch for making eddy covariance measurements. It is very flat and has prevailing winds that are channeled from the west through the Carquinez Strait. The water table is about 0.7 m below the surface (Deverel and Rojstaczer, 1996), but subsurface irrigation via a network of spud ditches brings the water table to the surface. This periodic irrigation activity provides a unique opportunity to study changes in the water table faster than they would naturally occur and evaluate their effect on gas fluxes.
throughout the growing season. Sherman Island is an ideal location for this research because of its key location across the estuary salinity gradient (see Figure 3-1). Sherman Island is often near the maximum salinity intrusion line (i.e., 1000 parts of chloride per million parts of water, 1.5 hours after high tide), and so in addition to its importance for water resources planners, it also receives seasonal and inter-annual variability of salinity inputs, making it a useful location to study the role salinity variations play on plant behavior.

The fluxes of CO₂ (NEE; μmol m⁻² s⁻¹), and sensible (H; W m⁻²) and latent heat (LE; W m⁻²) between the pepperweed infestation and the atmosphere were measured with the eddy covariance technique (Baldocchi, 2003). A micrometeorological tower within a fenced enclosure (to prevent cows from interfering with the instrumentation) was located in the pepperweed-infested southern part of the study site. The eddy covariance system was mounted on the tower on a 2.5-m boom oriented toward the West, the prevailing wind direction. The homogenous upwind fetch extends more than 3000 m over peatland pasture. Fluctuations in zonal, meridional, and vertical wind velocities (u; v; w; m s⁻¹), speed of sound (v_sound, m s⁻¹), and sonic temperature (T_sonic; °C) were measured with a sonic anemometer (Gill WindMaster Pro; Gill Instruments Ltd; Lymington, Hampshire, England). An open-path infrared gas analyzer (IRGA; LI-7500; LI-COR, Lincoln, NE, USA) was used to measure molar CO₂ (ρ_CO₂) and water vapor (ρ_H₂O) density fluctuations (mmol m⁻³). The high-frequency digital output from the two instruments was recorded by a personal computer at a scan rate of 10 Hz and stored as half-hourly block averages. NEE fluxes were separated into gross primary productivity (i.e., carbon uptake) and ecosystem respiration (i.e., carbon release to the atmosphere) following the neural network approach of Papale and Valentini (2003).

![Sherman Island](image)

Figure 3-1: Post-Shasta Dam Maximum Salinity Intrusion Lines, modified from California Department of Water Resources Sacramento-San Joaquin Delta Overview (2007). Sources: State Water Resources Control Board Final EIR D-1485 1978; Department of Water Resources Division of Operations and Maintenance daily salinity records. Lines represent annual maximum salinity intrusion, defined as 1000 parts of chloride per million parts of water, 1.5 hours after high tide.

3.3.2 Leaf water potential measurements
Predawn leaf water potential is a useful and widely used surrogate of the soil water potential of the wettest part of the root-zone, and effectively uses the plant itself as a sensor to determine the state of water in the soil (Richter, 1997). This technique depends on the assumption that for a non-transpiring plant where gravitational and frictional potential are negligible and there is no
transpiration to force a root-to-leaf potential difference, the plant’s water potential will equilibrate with its substrate. Some analysis has shown disequilibrium between plant and soil water status (Donovan et al., 2001; Donovan et al., 1999; Sellin, 1999), with suggested mechanisms including nocturnal transpiration, hydraulic lift in the root system, lack of time to reach equilibrium due to low plant hydraulic conductance, nighttime growth effects, and apoplastic solute accumulation in the leaves or roots. This final mechanism is of special interest for the study of halophytes such as pepperweed that may be more capable of taking up sodium and other ions to maintain water potential gradients and leaf turgor. However, in this case, the leaf water potential should be in equilibrium with the sum of osmotic and matric potentials in the soil, which provide the maximum relevant water potential from which the leaves must extract soil water. Finally, experiments using split pots with walnut saplings indicate that predawn leaf water potential can equilibrate with the wettest soil accessed by only 20% of the roots (Améglio et al., 1999), which is particularly relevant for a landscape such as the peatland pasture under study, where a saturated soil layer underlies a very dry surface layer.

The water potential of pepperweed leaves and stems was measured in two ways: from a Scholander-type pressure chamber (Soil Moisture, Inc.) and from a dew-point potential meter (the WP4, Decagon Devices). Measurements were taken weekly to monthly through the growing season of 2008. Predawn, mid-morning, mid-day, and late-afternoon samples were taken from a variety of leaves near the flux tower.

The WP4 operates according to the dew point method, which relates the sample water potential to the vapor pressure of air in equilibrium with the sample. Equilibrium is reached within 5-10 minutes of sealing the sample in a chamber with a chilled mirror. The chilled mirror allows a reading of the dew point, which occurs at the saturation vapor pressure. The headspace vapor pressure and sample temperature then give the water potential of the sample.

WP4 Leaf measurements are generated according to the methods described in Decagon’s Application Note on the WP4 (Decagon Devices, 2006). Briefly, a leaf is removed at its base from the plant with a scalpel. A drop of distilled water is placed on the leaf surface, and the leaf is abraded with a 5 cm x 2 cm piece of 600 grit sandpaper rubbed gently and evenly across both sides of the leaf surface. The leaf is dried with a lint-free tissue (Kimwipe) to remove water. The scalpel is used to cut the leaf into a circle that covers the base of the 40 mm diameter sample cup. Once placed in the cup, the sample is inserted into the chamber and sealed once the sample temperature is within 0.5°C of the unit block’s temperature. Samples are run in continuous mode for at least 25-30 minutes or until an approximate stability is reached. Prior to any samples run on the machine a calibration against standard KCl solutions is performed.

Leaf osmotic potential is determined by using leaves that have been frozen for at least 24 hours since removal from the plant. The freezing and thawing process breaks open cellular membranes, which eliminates the turgor pressure. There is a mix of freezing techniques used in the literature during field experiments – other scientists use liquid nitrogen to freeze the leaf, some just use a freezer at -20 °C (Fan et al., 2008). All of the samples presented in this study were kept in a standard freezer for 24 or more hours, and some were initially frozen with dry ice to reduce the temperature further.

Leaf turgor (\(\psi_t\)) and osmotic (\(\pi_{\text{leaf}}\)) potential added together yield the leaf water potential as measured in either pressure method (the WP4 or pressure chamber):

\[
\psi_t = \psi_l - \pi_{\text{leaf}}
\]  

[57]
Osmotic regulation is a widely studied mechanism by plants to withstand water or salt stress (Morgan, 1984), and is particularly of interest as a survival strategy for halophytes (Koyro, 2006; Suárez et al., 1998). Higher leaf solute levels may result naturally, and exist at full hydration, and may also be increased through solute accumulation as a response to water stress. The responsive case is known as osmotic regulation and helps maintain water potential at levels similar to turgor pressure and so allows continued plant growth.

Osmotic and turgor potential relations are complex and hard to generalize – the speed of onset of water or salt stress, the timing within a season, the species, part of plant, and other environmental conditions may play a role in the balance of these leaf pressures. In our data, as will be seen, the osmotic potential varies between approximately -1.5 MPa and -2.5 MPa but without a clear pattern relative to overall field leaf water potential.

3.3.3 Soil characterization
Soils at the Sherman Island peatlands site were analyzed for basic physical characteristics. These characteristics are summarized in Table 3-2, and the methods and individual results for determining them are given in Appendix C. Past measurements (Deverel and Rojstaczer, 1996) of soil bulk density (0.85) and organic matter content (28.0%) on Sherman Island in 1990-1991 are comparable to our measurements, though indicate that other parts of the island (i.e., in the wheat-growing area towards the south end) may have more organic matter. The age of this other measurement set may prevent its direct comparison due to soil carbon oxidation in the meantime.

Table 3-2: Summary of soil characteristics

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Range or Certainty</th>
<th>Method</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil texture</td>
<td>Clay loam or Silt loam</td>
<td>%sand: 23.1-29.2, %clay: 21.7-28.5, %silt: 42.3-55.1</td>
<td>Hydrometer/Stokes’ settling velocity</td>
</tr>
<tr>
<td>Near surface dry bulk density</td>
<td>1.09-1.3 g/cm³</td>
<td></td>
<td>Gravimetric tin sample $\rho_b = \frac{M_s}{V_t} = \frac{M_{drysoil}}{V_{tin}}$</td>
</tr>
<tr>
<td>Sub-surface dry bulk density</td>
<td>0.969 g/cm³</td>
<td>Std. dev: 0.256 (n=30)</td>
<td>Gravimetric tin sample</td>
</tr>
<tr>
<td>Particle density</td>
<td>2.25 g/cm³</td>
<td>Std. dev: 0.20 (n=18)</td>
<td>Volumetric displacement in water</td>
</tr>
<tr>
<td>Porosity</td>
<td>~50%</td>
<td>45-76%</td>
<td>Gravimetric tin sample, estimates of particle density</td>
</tr>
<tr>
<td>Soil retention parameters (Clapp-Hornberger)</td>
<td>$\psi_s$=-0.542 MPa, b=2.87</td>
<td>n=58 points, $r^2=0.375$</td>
<td>Measured on WP4, curve fit in matlab; $\psi = \psi_s S^b$</td>
</tr>
<tr>
<td>Soil retention parameters (Simplified Van Genuchten)</td>
<td>$\alpha_{SG}=1.528$, $n_{SG}=1.33$</td>
<td>$r^2=0.724$</td>
<td>Measured on WP4, curve fit in matlab; $S=(1+\alpha_{SG}h)^{n_{SG}}(1-\alpha_{SG}h)^{-1/(1-n_{SG})}$, where $h$ is in cm (or MPa*10⁻⁴)</td>
</tr>
</tbody>
</table>

3.3.4 Soil moisture, temperature, and electrical conductivity
Decagon Devices ECH2O-TE and ECH2O-5TE probes were used to measure soil moisture content, soil temperature, and bulk electrical conductivity. Detailed descriptions of the data-
extracellular and calibration processes are provided in Appendix B. Six ECH2O-TE probes were installed from May to October 2008, in a vertical profile with depths [80, 40, 20, 10, 5, 2.5 cm]. Because these probes gradually corroded in the organic, saline, wet soil conditions, they were removed and replaced. Eight ECH2O-5TE probes were installed from December 2008 to February 2009 12/2/08, in two vertical profiles: one with probes at depths [80, 40, 20, 10, 5, 2.5 cm], and another with probes at depths 10 and 2.5 cm. A new, improved set of ECH2O -5TE probes installed in March 2009 also had two vertical profiles with probes at depths [71, 36, 18, 9 cm] and [64, 32, 16, 8, 4, 2 cm].

3.3.5 Leaf area index
In this study $L_{AI}$ is measured with a Licor-2000 plant canopy analyzer at 10 m intervals in a 550 m transect on DOY 192 (of 2008). This transect provided a mean $L_{AI}$ of 0.62 m$^2$ m$^{-2}$, and a near-tower mean of 1.08 m$^2$ m$^{-2}$. Weekly to bi-weekly measurements of $L_{AI}$ on a similar transect were taken during the 2009 growing season. Monthly destructive plant clipping also provides some random spatial sampling of leaf area and phenology.

3.4 Field data results
The time of year chosen for the model (the 2009 growing season) is supported by repeated field measurements of leaf characteristics, and includes the period where pepperweed is at or near its maximal extent. Water table depth in the enclosure containing eddy covariance equipment during this period is approximately 50 cm (as measured by a pressure transducer in a well adjacent to the flux measuring equipment and checked by hand with a Solinst Co. water level meter approximately weekly). Water table depth reached up to 81 and 96 cm at two wells within the flux tower fetch depending on timing of irrigation flows. Some of the key forcing and validation data from the FLUXNET site over the period of interest is presented in Figure 3-2.
Soil moisture, temperature, and solution salinity taken from ECH2O-TE and ECH2O-5TE soil probes are presented in Figure 3-3 and Figure 3-4, respectively, and describe data calibrated and analyzed according to the methods in Appendix B. These data demonstrate that a shallow saturated zone (within 40 cm) underlies a dry surface layer. This relationship is held relatively constant throughout the summer growing season for both 2008 and 2009. Soil water and EC data are gap-filled using simple linear interpolation during the non-rainy season, since the values are relatively constant. Differences in VWC from year to year derive from differences in calibrating these probes; the ECH2O-TE probes were subject to corrosion and other errors due to the high organic content and saline conditions of this field site.
Figure 3-3: ECH\textsubscript{2}O-TE probe results: volumetric water content, soil temperature, and solution electrical conductivity at six depths during 2008 growing season. Because probes failed during data collection, some depths are not represented through the time-series, and sudden spikes are removed before use in model. Probe calibration and data analysis methods are described in Appendix B. Different readings of water content between 40 cm and 80 cm are probably artifacts of probe calibration or local electrical conductivity differences. The probe at 80 cm is in a saturated soil region.
3.4.1 Leaf water potential
Leaf water potential estimates from the pressure chamber and the dewpoint potential meter were similar, and are combined for display in Figure 3-5. Median predawn water potential ranged from -0.49 to -0.71 MPa, median morning water potential ranged from -0.74 to -2.25 MPa, and median afternoon water potential ranged from -1.3 to -2.24 MPa. The predawn water potential measurements are comparable to modeled soil potential weighted across the soil profile (see Figure 3-12 and Figure 3-15; for DOY 175-185, 2009, $\psi_s$~0.7 MPa, $\pi_s$~0.2 MPa).

Figure 3-4: ECH$_2$O-5TE data for March-November 2009 at the Sherman Island, CA field site.
3.4.2 Plant conductance estimate

The daily maximum, near midday ET rate is divided by the difference between pre-dawn and mid-day leaf water potential to derive a crude estimate of whole plant conductance $k$, as per Franks et al. (2007), Bunce (2006), and Duursma et al. (2008). Median values of predawn and midday water potential are used for the four days where predawn water potential measurements
are made. The estimated conductance is presented in Figure 3-7. There is a small decline in the whole plant conductance from approximately 4.8 mmol m⁻² s⁻¹ MPa⁻¹ in mid-summer to approximately 3.6 mmol m⁻² s⁻¹ MPa⁻¹ towards the end of the growing season.

Figure 3-7: Estimates of whole-plant conductance from midday ET rates and midday-predawn water potential difference. ET measurements are derived from latent energy fluxes determined by eddy covariance and water potential measurements are median values from estimates from both the dewpoint and pressure chamber techniques.

3.4.3 Comparison of modeled soil water potential and predawn leaf water potential

Soil water potential over the soil profile varies from very high soil matric potential and very low osmotic potential near the dry surface to near or fully saturated soil conditions with higher osmotic potential and lower matric potential from 30 to 60 cm below the surface. A sample soil profile demonstrating this variation is given in Figure 3-8, which for convenience of interpretation displays the data in both linear and logarithmic scales. At the near surface, with VWC<0.05, osmotic potential is near zero as so little water is in solution, but matric potential is high (~10⁶ kPa). In the near-saturated zone below 30 cm, matric potential approaches $\psi_{sat}$, at ~500 kPa, while osmotic potential reaches 290 kPa.
Figure 3-8: Soil matric and osmotic potential through the soil profile for DOY 121, 2009, given in both linear and log scales. These data are measured with the ECH₂O-5TE probes and analyzed according to Appendix B.

3.4.4 Light penetration model and Leaf Area Index
Measurements of incoming, reflected, and incoming diffuse PAR are used to parameterize the light equation penetration model presented in equations [47] through [55]. The canopy over which these instruments observe is more protected than the field at large, so has a higher $L_{AI}$ than the rest of the field. Therefore, this site provides a convenient upper limit for $L_{AI}$ and allows for a calibration of the model and partition of PAR into direct and diffuse components. The leaf angle parameter $\chi$ and $L_{AI}$ can be fit to the model (which was determined relatively insensitive to small changes in $k_d$). These parameters are determined on a daily basis by best-fit of the modeled PAR albedo against the half-hourly measured PAR albedo (which is ratio of the measured outgoing PAR against the measured incoming PAR), using the local optimization function fmincon in Matlab (Mathworks, Inc.). The model was tested for days 70 to 255 of the year 2009, when pepperweed is growing and the measured data is of higher quality than in 2007 and 2008. The calibration parameters and fitness are shown in Figure 3-9, and an excerpt of the time series is presented in Figure 3-10 to demonstrate the closeness of the model to the dataset. The leaf angle parameter $\chi$ has a relatively constant value near 0.72, and $L_{AI}$ during the second half of the season is relatively constant with a mean of 3.03. Both of these estimates are consistent with observations: pepperweed’s leaves are largely horizontal, though this can change especially in the upper canopy, and at times with wind. The $L_{AI}$ under the PAR equipment is generally greater than the field at large, where mowing and cattle movement and grazing reduce vegetative cover.
Figure 3-9: Fitted parameters from irradiance model. $L_A$ and $\chi$ are fit using the root-mean-square (RMSE) difference from half-hourly daily PAR albedo measurements. In the center plot, the LAI estimates in black are best fit estimates from the radiation model. The red circles represent transect-average plant-area-index measurements from the Licor-2000, and the red dotted line is a simple linear interpolation/extrapolation from the Licor-2000 measurements used in SVAT model evaluations.

Figure 3-10: Daily $L_A\chi$ model parameterized and fit to PAR albedo measurements for four days in 2009.

3.5 Modeling Results
The model is run over the 2009 growing season with and without accounting for soil salinity-induced osmotic potential. Modeled plant transpiration and carbon uptake for this period are
compared to eddy covariance-derived estimates of gross primary productivity and evapotranspiration, first in terms of daily average values (Figure 3-11). Daily maximum stomatal conductance and minimum leaf pressure are shown for this period in Figure 3-12. The difference between including salinity or not is small relative to some other errors in model parameterization (or structure) but is not negligible. Over the 2009 season, plants under the saline model are predicted to use 8% less water and take up 10% less carbon than plants not facing soil salinity.

Figure 3-11: Daily average GPP and ET model results, 2009. Root-mean-square error between modeled and measured fluxes is provided in figure legend; total and mid-season (DOY 138-210) total flux amounts are also provided in the figure.
Figure 3-12: Daily maximum stomatal conductance and minimum leaf water potential for 2009. The daily minimum modeled soil matric pressure is provided in the lower panel.

Errors in the comparison between model and data are in part explained by poor estimation of $L_{AI}$, particularly at the start and end of the growing season. The root-mean-square error of daily ET estimates is correlated to $L_{AI}$ with $r^2=0.42$ ($p<0.001$), while the error in GPP estimates has no significant correlation to $L_{AI}$ (Figure 3-13). Despite this lack of correlation, it is clear that when $L_{AI}$ is assumed to be below approximately 0.6, the probability of a large error in daily GPP estimates is increased.

Figure 3-13: Model errors in daily ET estimates are significantly ($r^2=0.42$) correlated to $L_{AI}$; model errors in daily GPP estimates are not significantly correlated to assumed $L_{AI}$. 

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A subset of the annual time series is investigated to check whether the model adequately represents the diurnal behavior of the ecosystem (Figure 3-14; Figure 3-15). For most days of this period, model-derived estimates of ET are close to measured estimates, with a slightly closer fit in the cases where soil salinity is included. Modeled estimates of GPP, on the other hand, are further from measurement-derived estimates, though again show a closer fit from the saline cases than from the case where salinity is ignored. The contribution to overall fluxes from the shaded portion of the canopy is presented within Figure 3-14; the shaded portion supplies 2-6% of canopy evaporation and 8-18% of canopy carbon uptake. There is a negligible difference between the model results with and without salinity in terms of the relative contribution of the different canopy types. Modeled leaf potential slightly underestimates measured midday leaf potential (taken in 2008), but generally captures the diurnal changes in leaf pressure needed to drive evapotranspiration fluxes.

The model significantly underestimates ET and GPP during days 178 and 179. These days are unique in this ten day period in having air temperatures exceed 35 °C (other days reached 30 °C temperatures), and in having the vapor pressure deficit at 4.6 kPa (other days tended to have deficits less than 2.5 kPa). The model is parameterized such that these increased input values reduce $g_s$ and $\psi_l$, and so underestimates evapotranspiration and net assimilation.

Attention is therefore focused toward the $D_x$ parameter governing reductions to stomatal conductance given increasing vapor pressure deficit equation [11]. Initial model runs where this parameter is increased, to reduce the effect of stomatal conductance are suggestive that this parameter should indeed be allowed to increase. However, increasing this parameter’s value does not uniformly increase model fitness: Figure 3-16 contains an initial sensitivity analysis of this parameter’s influence on the root-mean-square error of both ET and GPP. Increasing $D_x$ does reduce the modeling error for the subset period, but appears to increase the model’s error when analyzed over the whole growing season. This result may change once a better set of $LAI$ estimates is used, though may also depend on more accurate estimation of other parameters (such as the slope term $a_f$ of the Ball-Berry equation). This finding will be investigated in further detail in the following chapter, which focuses on the model’s sensitivity to its governing parameters.
Figure 3-14: ET and GPP ($A_n$) model results for subset period (DOY 175-185, 2009).
Figure 3-15: Stomatal conductance and leaf water potential for subset period (DOY 175-185, 2009) for two models. Data gaps derive from night-time conditions, which are not modeled. Leaf water potential is compared to minimum modeled soil matric pressure for comparison.

Figure 3-16: Model fit dependence on $D_x$ parameter (see equation [11]). Model results above assume a $D_x$ value of 1.50 kPa; here model fitness is presented for various values of $D_x$ for two time periods: the subset period (DOY: 175-185) and the whole 2009 growing season as modeled above.
3.6 Discussion

3.6.1 Assessment of model results

The key findings of this chapter are (1) that the SVAT model framework can be extended to incorporate the effects of soil osmotic potential on leaf-level gas exchange and field-level fluxes, (2) that incorporating soil salinity into the model predicts 8% less water use and 10% less carbon uptake than without salinity, (3) that the relatively simple characterization of $L_{AI}$ (as a field-mean estimate taken from a transect of Licor-2000 measurements) works well for the middle part of the year, but not for the earlier or later part of the year, and (4) that initial sensitivity analysis suggests pepperweed leaves are less sensitive to high vapor pressure deficits than previously assumed from leaf-level measurements.

The model presented is successful at capturing seasonal and diurnal changes in leaf transpiration and carbon uptake for periods where we have greater confidence in $L_{AI}$ values. Estimates of $L_{AI}$ in the early and late part of the year are less certain, and may be influenced by measurement errors relating to lower canopy heights and/or greater spatial variability. The role of spring grasses in the field may be one significant factor in creating this uncertainty in $L_{AI}$. The spatial variability at the field site even influences the relevance of potentially useful continuous measurements: the tower boom containing incoming and reflecting PAR sensors may cover a ‘footprint’ that is more vegetated than the field at large (Figure 3-9). An expanded look at the model’s sensitivity is forthcoming in Chapter 4 and can be used to suggest $L_{AI}$ estimates for the periods where its poor accuracy prevents good model results. Future work will extend the SVAT model results to cover additional measurement periods (i.e., 2007 and 2008), which suffer from poorer soil moisture characterizations but benefit from other field measurements (such as the leaf-level parameters derived in Chapter 2). Additional sources of uncertainty may derive from the eddy covariance derived data: first, the flux partitioning between GPP and ecosystem respiration may be inaccurate at higher temperatures, where there are fewer data points to constrain these estimates; second, incomplete closure of the energy balance may contribute to errors in evapotranspiration and stomatal conductance estimates (Wohlfahrt et al., 2009).

The effect of soil salinity is represented in this model, and demonstrates that even in near saturated lower-profile soil conditions, osmotic pressure may reduce evapotranspiration and carbon uptake by increasing plant stress. Regions with different soil conditions may be similarly modeled to predict how drier or wetter soil conditions may influence the role of salinity on plant water use. In this field site, the model predicts a 10% reduction in carbon uptake (and so, plant growth) and an 8% reduction in plant evapotranspiration. These changes appear small when compared to some of the natural variability in these fluxes, but when cumulated across the growing season could have real implications for regional agricultural productivity and water resources decisions. In this field site, the near-surface water table may allow pepperweed to offset some of the osmotic pressures from soil salinity levels with the general ease of water acquisition. These pressures still exert a stress on the leaves, through increased leaf water potential, and so influence the water and carbon fluxes. In a drier location, or with a species less salt-tolerant, the role of soil salinity is expected to be greater in modifying these fluxes.

3.6.2 Model Context and Applicability

The model developed and evaluated in this chapter can be used to depict the influence of soil salinity on plant water use and photosynthesis. As a result, its application should be relevant to a variety of users, who should also benefit from the sensitivity analysis and parameterization.
studies in the proceeding chapter. While other root water uptake models account for the effects of atmospheric carbon dioxide, for rock weathering processes, for multi-ion effects, and for groundwater and surface-water interactions, and are more physically representative for doing so, our relatively simple model is still able to capture the diurnal cycle in transpiration and carbon uptake. Our model allows a relatively straightforward approach to salinity modeling, and because of the small amount of forcing data needed, it is particularly appealing to those working in the developing world, where such information is scarce. Given climatological assumptions for the radiative forcing conditions, sine-governed diurnal cycling, reasonable initial conditions for soil moisture, and air temperature and humidity data, this model could feasibly represent agricultural and grassland systems. The treatment of salinity as an additive process in the soils reduces some of the calibration needs inherent in the multiplicative S-shaped models but without sacrificing a realistic physical interpretation of the effects of salty soils. The results presented here demonstrate and quantify the importance of osmotic pressure on plant transpiration, which is a crucial part of any water budget. This work should be of assistance to those interested in root water uptake, irrigation efficiency, irrigation drainage water quality, and water resources management.

The stomatal sub-models account for the dependence of stomatal conductance on photosynthesis, so they allow for a more complete relationship between soil water and salinity conditions and plant carbon uptake and growth. Incorporating photosynthesis into the water transport model requires plant-specific calibration for terms such as $V_{cmax}$ (maximum carboxylation rate) and $J_{max}$ (maximum electron transport rate). These terms can change when a plant faces salt stress due to ionic toxicity effects in the leaf (James et al., 2006; Muranaka et al., 2002), but the functional form of these changes is currently unknown. These toxic effects result from the gradual accumulation of plant concentrates in older leaves, which derive from the small portion of soil salts unexcluded by the roots. While some of these ions are compartmentalized in leaf or stem vacuoles, eventually the vacuole capacity is exceeded, and salts build up in the cytoplasm and inhibit enzyme activity or accumulate in the cell walls and dehydrate the leaf. As plants devote more energy to salt stress, maintenance respiration increases, thereby reducing the effectiveness of converting carbon taken up during photosynthesis to plant matter and growth. Additionally, disrupting the ratio of sodium and potassium ions can damage enzymatic processes related to photosynthesis, and so reduce $V_{cmax}$ (Munns, 2005). Future discovery of the functional forms for salt effects on pepperweed’s leaf physiology will be of use in other studies of leaf-level responses to salt. The sensitivity analysis of the following chapter may guide representations of salt ionic toxicity effects on the photosynthetic terms and leaf-level mesophyll and stomatal conductances.

3.6.3. Potential for improvement
Aggregating many leaf- and plant-level processes to the field scale is difficult in any SVAT exercise. This task is particularly challenging in a landscape characterized by heterogeneous, noncontiguous vegetation. It is difficult, then, to rely on a single transect of $L_{AI}$ estimates through the measurement fetch, no matter how many measurements are taken. These estimates are subject to errors in measurement timing (such as through sub-optimal light conditions), in analysis (as they represent a plant area index which may include non-living or senescent material), and in their overall representativeness of site conditions. The $L_{AI}$ measured in the transect may not, for example, capture small areas of highly active plants. On the other hand, the $L_{AI}$ measured by the Licor-2000 is more accurately described as a plant-area-index, and so may
account to some extent for some representation of cuticular conductance as well as scaling the more important stomatal conductance.

This model is evaluated at Sherman Island with a high level of information: multiple years of eddy flux data, significant understanding of soil characteristics, plant behavior, and high frequency meteorological data. As such, evaluation of the model at this site allows an expansion of the model of plant responses to salinity levels to apply under broader circumstances. This research demonstrates that including representations of salinity into SVAT-type models can change ET flux predictions by at least 8%; this value may change under drier soil conditions when the relative importance of osmotic pressure is increased or under wetter soil conditions when dried salts are dissolved into the soil solution. Future modeling efforts can take the form of more accurate mechanistic understanding (and representation in the model) and parameterization. The parameters will not be constant in time, as is common in current water transfer models, but may be allowed to vary as functions of both phenological change and soil salinity levels. Working from data that covers more than one full year will guide future work into the role of inter-annual variability on regional gas fluxes and will benefit planners interested in long-term changes of Delta region land use.
3.7 Works Cited


Duursma, R. et al., 2008. Predicting the decline in daily maximum transpiration rate of two pine stands during drought based on constant minimum leaf water potential and plant hydraulic conductance. Tree Physiology, 28(2): 265.


Appendix A. The solution of the quartic expression for leaf temperature, following Nikolov et al. (1995), and referring to terms in equations [40] to [44] is given in the subsequent set of equations:

\[ y = a_t c_t - 4d_t \]  
\[ p = \frac{3y - b_t^2}{9} \]  
\[ Q = \frac{1}{54} \left( b_t (2b_t^2 - 9y) - 27(d_t (4b_t - a_t^2) - c_t^2) \right) \]  
\[ D_{scf} = (Q^2 + p^3)^{0.5} \]  
\[ y_2 = \exp \left( \frac{\ln(Q + D_{scf})}{3} \right) - \exp \left( \frac{\ln(D_{scf} - Q)}{3} \right) + \frac{b}{3} \]  
\[ R = \left( \frac{a_t^2}{4} + y_2 - b_t \right)^{0.5} \]  
\[ t_1 = \frac{a_t (4b_t - a_t^2) - 8c_t}{4R} \]  
\[ E = \frac{a_t^2}{2} - b_t - y_2 \]  
\[ T_t = \frac{a_t}{4} - \frac{R - (E - t_1)^{0.5}}{2} \]

Appendix B. Data analysis for ECH2O TE and ECH2O 5TE probes
Two sets of soil probes from Decagon Devices, Inc., were used in this study: the ECH2O-TE and ECH2O-5TE probes, which provide co-located estimates of soil temperature, soil electrical
conductivity, and soil water content. Calibration procedures followed Decagon’s suggestions and revealed that for the peatland soils of Sherman Island, the default equation for converting the raw dielectric signal to volumetric water content overestimates soil moisture. This section provides a summary of these calibration methods and their results, as well as descriptions of the soil temperature and soil electrical conductivity measurements also taken by these probes. Data were read into Campbell Scientific CR10x and AM416 Multiplexer.

The 5TE probe measures the bulk dielectric permittivity, $\varepsilon'_b$, which is directly proportional to Raw VWC counts:

$$\varepsilon'_b = \frac{\text{VWC}_{\text{Raw Counts}}}{50} \quad [1]$$

Probes previous to October 2008 were the older ECH2O-TE probes, which give different outputs to the ECH2O-5TE probes. In particular, the raw output value for the water content term, Raw, relates to the bulk dielectric constant of the water soil medium through the following cubic equation:

$$\varepsilon'_b = 7.64 \times 10^{-8} \times \text{Raw}^3 - 8.85 \times 10^{-5} \times \text{Raw}^2 + 4.85 \times 10^{-2} \times \text{Raw} - 10 \quad [2]$$

Raw dielectric permittivity values are converted to soil water content through a model derived from laboratory experiments on soils from Sherman Island. The null hypothesis is that the Topp equation (Topp et al., 1980) is sufficient to fit volumetric water content to the measured dielectric constant. This equation is a third-degree polynomial fit to data from four mineral soils, and is commonly used with field measurements (Nadler, 2005):

$$\theta = -5.3 \times 10^{-2} + 2.92 \times 10^{-2} \varepsilon'_b - 5.5 \times 10^{-4} \varepsilon'_b^2 + 4.3 \times 10^{-6} \varepsilon'_b^3 \quad [3]$$

Soil-specific data were derived by incrementally increasing the soil moisture from a batch of soil. This soil’s volumetric water content was determined by using the volumetric soil sampler method, where a tin of known volume is used. Two tin measurements are made for each soil moisture level. The soil is stirred to increase homogeneity; probes are placed in two positions in the soil mix for each soil moisture level. The mean dielectric constant read for each soil moisture level is compared to the mean volumetric water content determined by the tins and third-degree polynomials are fit to the data for each probe. Fitting this dataset reduces the root-mean-square error from the Topp equation, as is evident in Figure B-1: and Figure B-2.
Figure B-1: Soil water content calibration, ECH2O-TE probes used 2008. Different symbols represent individual probes, whose data are merged to determine the overall best-fit.

Figure B-2: Soil water content calibration of the ECH2O-5TE probes, used in Sherman Island from late 2008 to present.

The probe raw temperature values $T_{raw}$ are converted to °C using the algorithm:

$$T(°C) = \frac{T_{raw} - 400}{10}$$  \[4\]

The sensors measure the raw electrical conductivity of the bulk medium surrounding the probe. This raw value is converted to units of dS/m via the following compression algorithm:
The measured bulk EC can be converted to pore EC (Hilhorst, 2000):

\[
EC\left(\frac{dS}{m}\right) = \frac{\sigma_{raw}}{100} \quad \text{if } \sigma_{raw} \leq 700
\]

\[
EC\left(\frac{dS}{m}\right) = \frac{700 + 5(\sigma_{raw} - 700)}{100} \quad \text{if } \sigma_{raw} > 700
\]

The measured bulk EC can be converted to pore EC (Hilhorst, 2000):

\[
\sigma_p = \frac{\varepsilon'_p\sigma_b}{\varepsilon'_b - \varepsilon'_{\sigma_b=0}}
\]

Where \(\sigma_p\) and \(\sigma_b\) are the pore and bulk water electrical conductivities (dS/m), respectively; \(\varepsilon'_p\) and \(\varepsilon'_b\) are the real portion of the dielectric permittivity (unitless) of the soil pore water and bulk soil, respectively; \(\varepsilon'_{\sigma_b=0}\) is an offset term representing the real portion of the dry soil’s dielectric permittivity. Decagon recommends using a value of 6, while Hilhorst (2000) recommends using 4.1. Soil temperature measurements allow \(\varepsilon'_p\) to be calculated:

\[
\varepsilon'_p = 80.3 - 0.37 \times (T_{soil} - 20)
\]

Where \(T_{soil}\) is the soil temperature (ºC) measured by the ECH2O-5TE probe.

The solution EC, which is equivalent to the electrical conductivity of pore water removed from a saturated paste, can be determined by using the measured volumetric water content and the soil’s (pre-determined) porosity (Groenevelt et al., 2004):

\[
\sigma_{solution} = \frac{\sigma_p\theta + \sigma_d(\Phi - \theta)}{\Phi}
\]

Where the electrical conductivity of distilled water, \(\sigma_d\), is assumed to be 0 dS/m, and the porosity \(\Phi\) can be determined through the soil’s bulk density \(\rho_b\) by assuming the material density \(\rho_s\) is 2.65 Mg m\(^{-3}\):

\[
\Phi = 1 - \frac{\rho_b}{\rho_s} = 1 - \frac{\rho_b}{2.65}
\]

Appendix C. Soils information for Sherman Island peatlands site

C.1. Soil texture:

Soils from Sherman Island were analyzed for Soil Texture according to standard hydrometer methods (Gee and Bauder, 1986). These methods depend upon Stokes’ Law for settling particles, and are a function of the specific hydrometer type and cylinder used for analysis. Briefly, the method is as follows:

Approximately 50 g of dry-soil equivalent were mixed with 100 mL of HMP solution and approximately 250 mL of de-ionized water, mixed and allowed to soak overnight. The sample is then quantitatively transferred to a mixing cup and blended for 5 minutes to ensure dispersion. It is then transferred in whole to the settling cylinder, which is filled to 1 L with de-ionized water. After the final transfer an hour is allowed to let the suspension equilibrate thermally. The cylinders were mixed with a plunger to dislodge any sediment and to create a uniform mixture. Following careful insertion, hydrometer readings were made at 30 seconds, 60 seconds, 1.5 hours, and 24 hours. All parameters have been temperature corrected and compared to a “blank” column of de-ionized water. Separate hydrometers were used for each column to avoid any mixing or sample disturbance in hydrometer reinsertion.

The summary of results from this method is shown in Table C-1, where the samples are shown to be between a silty and clay loam.
Table C-1: Results of soil texture analysis from Sherman Island soils.

<table>
<thead>
<tr>
<th>Sample</th>
<th>% sand (&gt;50 µm)</th>
<th>% clay (&lt;2 µm)</th>
<th>% silt (2 - 50 µm)</th>
<th>Classification Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sieved soil, surface 30 cm,</td>
<td>29.2</td>
<td>28.5</td>
<td>42.3</td>
<td>Clay loam</td>
</tr>
<tr>
<td>Collected Jun ’08</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10-20 cm, 7/28/08 collection</td>
<td>28.7</td>
<td>25.6</td>
<td>45.8</td>
<td>Loam</td>
</tr>
<tr>
<td>60 cm, 7/28/08 collection</td>
<td>23.1</td>
<td>21.7</td>
<td>55.1</td>
<td>Silty Loam</td>
</tr>
</tbody>
</table>

C.2. Bulk Density

At Sherman Island volumetric tin samples of soil moisture were collected on several different days. The bulk density results are presented (Figure C-1) with a consistent mean between 1.2 and 1.24 g/cm$^3$ for near-surface samples near the six soil moisture probes.

![Figure C-1: Bulk Density (Oct 11, 2007 and Oct 25, 2007, respectively) near surface](image1)

Results from tin samples at six depths in five different profiles are presented in Figure C-2.

![Figure C-2: Bulk Density (Nov 8, 2007) for 5 soil profiles (samples at six depths)](image2)


C.3 Particle density
Eighteen soil samples were analyzed for particle density by immersion into water in a graduated cylinder and measuring the water’s displacement. Measurements were performed on soils taken from the surface layer of the field site on October 11, 2007. The average particle density was found to be 2.25 g/cm\(^3\), with standard deviation 0.20 g/cm\(^3\).

C.4 Porosity
Soil porosity \(\Phi\) is measured using the equation: \(\rho_b = (1 - \Phi)\rho_s\), where \(\rho_s\) and \(\rho_b\) are the soil particle and dry bulk densities, respectively. These measurements are performed in the soil profile for the same set of soils analyzed in Figure C-2, and these results are presented in Figure C-3. The porosity is shown to increase at depth, though this may be an “apparent” change falsely revealed by concurrent changes in soil particle density (which could be reduced as a result of the increase in soil organic material).

![Porosity by Depth, Nov 8, 2007](image)

**Figure C-3: Porosity by depth, 11/8/07, assuming particle density of 2.25**

C.5 Soil retention curve
The soil retention curve is based on 58 measurements in the WP4 Dewpoint Potentialmeter (Figure C-4). These measurements include both soil matric and soil osmotic pressure; a future task is to separate these pressures based on measurements of the soil’s electrical conductivity (which can be converted to units of salinity-based osmotic pressure). The curves fit to the data do not separate the wetting and drying samples (i.e., the hysteresis effect is not explicitly considered here), though drying samples do show a tendency to have a more negative pressure head than wetting samples. The degree of saturation is determined using a porosity of 50% and a bulk density of 1.2 g mL\(^{-1}\) to convert from mass water content (which is the mass of water divided by the mass of wet soil):

\[
S = \frac{VWC_{sample}}{\Phi} = \frac{\rho_b}{\Phi} \ast MWC = \frac{1.2}{0.5} \ast \left(\frac{\text{mass water}}{\text{mass wet soil}}\right)
\]

The data and lines of best fit to two common pedo-transfer functions (Clapp and Hornberger, 1978; van Genuchten, 1980) are provided in the figure, as are the Clapp-Hornberger
models for 9 common soil types, and a fit to peat soils data from the literature (Weiss et al., 1998). The simplified van Genuchten equation from Weiss et al. (Weiss et al., 1998) assumes pressure is a head $h$ (in cm) and ignores the residual water capacity in the original equation:

$$s = \frac{VWC}{\Phi} = \left(1 - \alpha_{vg}(h^n)\right)^{-1+\frac{1}{n}}$$

The Clapp-Hornberger model assumes $\psi_s = \psi_{sat} - b$, where $\psi_{sat}$ is the soil water potential at saturation, and $b$ is a fitting parameter. The 51 measurements from soils taken at Sherman Island led to best-fit Clapp-Hornberger parameters of $\psi_{sat} = -0.542$ (with standard error bounds between -0.425 and -0.690 MPa) and $b = 2.87 \pm 0.31$.

The apparent misfit of data to the curves at high saturation levels is exaggerated due to the logarithmic scale of the soil-pressure axis.

![Soil retention curve](image)

**Figure C-4:** Soil retention curve. Curves for different soils using the Clapp–Hornberger method are shown for comparison. The soils at Sherman Island are silt loam or clay loam, whose curves surround much of the data. The two curves fit to our soils are shown in green and magenta (representing the Clapp–Hornberger and a simplified van Genuchten). Error bars for the Clapp–Hornberger fit are shown; these should contain 50% of the values by standard error analysis.

### Appendix D. List of parameters used in the model

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Meaning</th>
<th>Dimension</th>
<th>Units if applicable</th>
<th>Relevant Equation(s)</th>
<th>Value if applicable</th>
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<tbody>
<tr>
<td>$a$</td>
<td>Root index correction term</td>
<td>-</td>
<td>-</td>
<td>[6]</td>
<td>8</td>
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<tr>
<td>$a_1$</td>
<td>Slope of Leuning-type equation</td>
<td>-</td>
<td>-</td>
<td>[10]</td>
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<td>$A_{c}$</td>
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<td>$\mu$mol m$^{-2}$s$^{-1}$</td>
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<td>Intermediate photosynthesis</td>
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<td>[23], [24]</td>
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<td>$A_n$</td>
<td>Net assimilation of CO$_2$</td>
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<td>$\mu$mol m$^{-2}$s$^{-1}$</td>
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<tr>
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<td>$\mu$mol m$^{-2}$s$^{-1}$</td>
<td>[20]</td>
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</tr>
<tr>
<td>$A_s$</td>
<td>Saturated (maximal) photosynthesis</td>
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<td>$\mu$mol m$^{-2}$s$^{-1}$</td>
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<td>Symbol</td>
<td>Variable Description</td>
<td>Unit(s)</td>
<td>Value(s)</td>
<td>Reference(s)</td>
<td></td>
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<td>-------------------</td>
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<td>[40],[41]</td>
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<tr>
<td>(A_{\text{g},\text{q},1})</td>
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<td>[40],[41]</td>
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<td>Plant conductance response shape parameter</td>
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<td>[5]</td>
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<td>(\mu\text{mol mol}^{-1})</td>
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<td>([\text{M L}^2\text{T}^{-2}]\text{M}^0\text{Θ}^1)</td>
<td>J kg(^{-1})\text{K}^{-1}</td>
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<td>(\mu\text{mol mol}^{-1})</td>
<td>[10],[12]</td>
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<td>[40],[41]</td>
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<td>m(^3)s(^{-1})</td>
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<td>(D_v)</td>
<td>Reference vapor pressure deficit</td>
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<td>kPa</td>
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<td>kPa</td>
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<td>mm day(^{-1})</td>
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<td>mm day(^{-1})</td>
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<td>mm day(^{-1})</td>
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<td>Function of vapor pressure deficit on stomatal conductance</td>
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<td>m s(^{-2})</td>
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<td>Function of projected area of phytoclements</td>
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<td>(g_{\text{bu}})</td>
<td>Conductance from leaf boundary to atmosphere</td>
<td>L T(^{-1})</td>
<td>m s(^{-1})</td>
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<td>Leaf boundary layer sensible heat conductance</td>
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<td>L [M L(^{-1})T(^{-2})]T(^{-1})</td>
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<td>(g_{\text{max}})</td>
<td>Maximum plant conductance</td>
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<td>Ground heat flux</td>
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<td>Wm(^{-2})</td>
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105
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Units</th>
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</tr>
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<tbody>
<tr>
<td>$g_{st, CO2}$</td>
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<td>mol L⁻² T⁻¹</td>
<td>µmol m⁻² s⁻¹</td>
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<tr>
<td>$g_r$</td>
<td>Soil-root conductance</td>
<td>L [M L⁻¹ T⁻¹]⁻¹ T⁻¹</td>
<td>µm MPa⁻¹ s⁻¹</td>
</tr>
<tr>
<td>$g_{sp}$</td>
<td>Soil-root-plant conductance</td>
<td>L [M L⁻¹ T⁻¹]⁻¹ T⁻¹</td>
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<td>L T⁻¹</td>
<td>m s⁻¹</td>
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<td>m s⁻¹</td>
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<td>Matric head</td>
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<td>$H_r$</td>
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<td>$I_c$</td>
<td>Whole canopy absorbed irradiance</td>
<td>mol L⁻² T⁻¹</td>
<td>µmol m⁻² s⁻¹</td>
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<td>$I_{sh}$</td>
<td>Shaded canopy absorbed irradiance</td>
<td>mol L⁻² T⁻¹</td>
<td>µmol m⁻² s⁻¹</td>
</tr>
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<td>$I_{Sun}$</td>
<td>Sunlit canopy absorbed irradiance</td>
<td>mol L⁻² T⁻¹</td>
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<td>$I_b$</td>
<td>Direct beam absorbed irradiance</td>
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<td>Scattered beam absorbed irradiance</td>
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Chapter 4: Model sensitivity and parameterization

4.1 Introduction

Previous results suggest that model uncertainty changes depending on the environmental conditions of the system it simulates. To assess the sources and magnitudes of this uncertainty, I apply a version of the Generalized Likelihood Uncertainty Estimation (GLUE) framework developed by Beven and Binley (1992) to suggest various parameter sets that generate reasonable “behavioral” fits to measured data using the soil-vegetation-atmosphere transfer model developed in the previous chapter of this dissertation. The sensitivity of agricultural and ecological systems to predicted changes in climate is an important and ever-expanding field of research. Complicating these efforts are the interacting effects of increased temperature, increased CO₂ levels, and changes in the temporal distribution of rainfall. A recent study attempting this level of sensitivity analysis (Ficklin et al., 2009) acknowledges the challenges in accurately modeling leaf-level processes: the well-used SWAT model (Arnold et al., 1998) may overestimate stomatal conductance reductions at high CO₂ concentrations, an error that carries through to estimates of evapotranspiration and regional plant water use (Eckhardt and Ulbrich, 2003). Similarly, results presented in Chapter 3 reveal uncertainties in parameters governing stomatal responses to the atmospheric vapor pressure deficit, and results of Chapter 2 demonstrate the uncertainties of parameterizing leaf gas exchange parameters.

The interaction between parameters, model forms, and specific climate or soil environments, is complex and difficult to assess. Monte Carlo frameworks have been used to assess the sensitivity of model outputs to changes in model input parameters (Demaria et al., 2007), though Bayesian analyses have often been considered too difficult to apply to complex environmental systems with many co-varying components (Beven, 2006b). The GLUE framework is useful (and well used) for finding different parameter combinations that are acceptable in reproducing the observed behavior of physical systems, and may yield insight into model improvement, sensitivity, and parsimony. GLUE is used under the assumption of model equifinality (Beven, 2006a), which acknowledges that there may be multiple acceptable models, and sorts between these by selecting behavioral parameter sets from many model realizations. While accepting some degree of equifinality, use of the GLUE framework should not be interpreted to imply that there is no globally optimal solution nor that such a goal is merely utopian.

These issues have been addressed before in models simulating both hydrological (Beven, 2006a) and eddy covariance (Medlyn et al., 2005; Mitchell et al., 2009) data. Medlyn et al. (2005) do a particularly good job explaining the difficulties in validating models with eddy covariance data, and focus their concerns on issues of equifinality, insensitivity, and uncertainty. Insensitivity may arise from the way diurnal variations in fluxes mask smaller effects of the driving variables, and so prevent adequate predictive modeling outside measured conditions. Uncertainty can result from parameter, model structure, and data error, and is especially important in the use of eddy covariance derived data because of the complexity of flux data retrieval and analysis. The GLUE analysis in this chapter is performed under two levels of aggregation (1-day and 3-day) to assess how this evaluation decision may influence parameterization and sensitivity determination. This chapter focuses on parameter uncertainty and model sensitivity, and when predictions about future conditions are made, potential model insensitivity is noted.
The SVAT model presented in Chapter 3 contains several parameters thought to be highly intercorrelated and difficult to predict without more focused measurement efforts in a greenhouse or controlled experimental analysis. These connected parameters generally fall into two partially overlapping categories: those which govern stomatal conductance directly and those which determine the effect of leaf pressure on plant processes. In the former set are $a_1$, the slope of the Ball-Berry equation, and $D_x$, the reference vapor pressure deficit controlling stomatal responses to low humidity levels. In the latter set are the scaling ($a$ and $y_0$) and shape parameters ($c$ and $s_f$) governing the implications of low leaf water potential on plant conductance, first, and photosynthesis, second. Because stomatal conductance also depends on photosynthesis (directly) and plant conductance (indirectly), all of these parameters are interconnected. Understanding the relationships between these parameters and their joint impacts on model outputs of interest should raise the model’s parsimony in its representation of actual physical processes (Buckley, 2005) and increase model relevance under a greater set of environmental conditions.

Of additional interest, and a driving motivator for this dissertation, is the model’s description of plant sensitivity to soil salinity conditions. Because model evaluation (i.e., Chapter 3) relies on data from a representative landscape containing low to mid-level salinity stress, numerical modeling and simulation offer an opportunity to predict how changes in salinity will influence plant-governed fluxes of water and carbon. These simulations allow a test of the hypothesis that seasonal average stress-factors, commonly used in salinity modeling (Shani et al., 2007), are sufficient to account for the role of osmotic stresses on plant behavior. They may also provide a useful guideline for analyzing salt tolerant (Chinnusamy et al., 2005; Yamaguchi and Blumwald, 2005) and halophytic (Rozema and Flowers, 2008) crop species and genotypes of increasing societal and research interest. The sensitivity of various species to soil salinity can also be useful to plan field leaching, irrigation, or crop scheduling accordingly. Moreover, describing plant responses to salinity in a manner that can be transferred to other modeling contexts may allow soil salinity effects to be represented in land surface or regional climate models.

Once a model’s sensitivity is understood, it can be used to examine different scenarios that consider a range of expected climates, environmental conditions, or management strategies. Long-term climate change is particularly important to consider, as great ecological responses have been predicted to follow changed annual temperature patterns, increased CO$_2$ levels, and changes in precipitation or soil moisture (Dukes and Mooney, 1999; McCarty, 2001; Smith et al., 2009). In California’s San Francisco Estuary, the general result of a warmer climate and associated seasonal changes in river outflow is expected to include greater salinity levels, particularly in the summer as flow is reduced, primarily from earlier snowmelt (Hayhoe et al., 2004; Knowles and Cayan, 2004; Vicuña and Dracup, 2007). This response may be greater than already modeled depending on the magnitude and occurrence of sea level rise (Cayan et al., 2008a). California’s Central Valley is predicted to experience vast changes in its hydrological regime, in its irrigation requirements, and in its agricultural yield (Ficklin et al., 2009). Past studies examining plant responses to salt salinity under doubled CO$_2$ found great reductions in water use, which was accompanied by reduced salt uptake by plants and osmotic pressures on the roots (Maggio et al., 2002). An assessment of predicted changes to weed species in this region should provide land managers with tools to understand more thoroughly some of climate change’s implications. Additionally these scenarios offer one perspective on testing the sensitivity of the model to new climate and atmospheric conditions.
In this context, there are three research objectives considered in this chapter that will increase understanding of the salinity-oriented SVAT model proposed in Chapter 3:

1) While searching for optimal or behavioral model parameterizations, what do we learn about the sensitivity of model parameters?

2) What do model simulations reveal about plant responses to different soil salinity conditions?

3) What does running this model under different climate change scenarios inform us about sensitivity to CO2 and temperature changes, and are salinity stresses modified in response to these changes?

4.2 Methods

4.2.1 GLUE scheme and parameter search

The Dynamically Dimensioned Search (DDS) algorithm is developed by Tolson and Shoemaker (2007) to find good global solutions to optimization problems, and scales the search process to the user-specified number of function evaluations. It starts as a global search algorithm that progressively becomes more local as the number of iterations approaches the maximum number \((m)\) of desired iterations, in a manner that roughly approximates a trial-and-error model calibration approach. The algorithm’s use in the GLUE framework is described in Tolson and Shoemaker (2008), and is given the name DDS–approximation of uncertainty (DDS-AU). The DDS-AU scheme finds behavioral parameter sets based on a pre-defined model acceptability threshold, and searches for locally optimal solutions deriving from different random seed parameter sets. This scheme greatly improves the efficiency of the GLUE algorithm (Beven and Binley, 1992), which traditionally relies on uniform random sampling. The DDS algorithm steps in pseudocode are repeated here for convenience (Table 4-1), and are updated to incorporate the additional steps used in the DDS-AU method.

The DDS algorithm is modified slightly to account for different sensitivities in the parameters under study. DDS Step 3 selects \(J\) of the \(d=1,\ldots,D\) decision variables to perturb in each iteration \(i\) by using the function \(P(i)=1-\ln(i)/\ln(m)\). Practically, this step is implemented by creating a vector \(p\) of uniformly sampled random numbers from 0 to 1, of length \(D\), and the variables where \(p^d\) is less \(P(i)\) are chosen as \(J\). Early modeling tests suggested that the objective function is more sensitive to certain parameters than others. In an effort to encourage the algorithm to focus attention on these parameters without weighting them through the whole search, a heuristic modification is suggested and applied. If changing a parameter \(d\) has reduced the objective function within the last three iterations, then \(p^d\) is reduced to \(p^{d'}\) prior to comparison with \(P(i)\) by the equation \(p^{d'}=p^d \cdot 2^{-k}\), where \(k\) is the number of reductions within any of the last three iterations. For instance, if a parameter \(d\) has been changed at iterations \(i-2\) and \(i-1\), and the function evaluation declined in value only after one of these iterations, \(p^d\) is halved, and so \(d\) is more likely to be chosen for perturbation in iteration \(i\). If a larger set of parameters has been changed at iteration \(i-1\), causing a reduction in the function evaluation, this whole set of parameters will have its probability \(p\) of inclusion reduced to increase the whole set’s probability of perturbation. Parameters more likely to reduce the objective function evaluation for this region of the parameter space are weighted towards further perturbation, thus driving a quicker solution. Using the previous three iterations to define this weighting keeps active parameters “in play” long enough so that the model may “try out” values which may either raise or lower the objective function’s evaluation value.
Table 4-1: DDS Algorithm, adapted from Tolson and Shoemaker (2007), Figure 1, updated to incorporate DDS-AU sampling (Tolson and Shoemaker, 2008).

**DDS-AU Step A.** Define AU inputs:
- Maximum total number of model evaluations for analysis ($N_{total}$)
- Desired number of behavioral samples to indentify ($n_{beh}$)
- Number of model evaluations per DDS optimization trial ($m_{DDS} \sim N_{total}/n_{beh}$)

**DDS-AU Step B:** Perform $n_{beh}$ DDS optimization trials from $n_{beh}$ random initial solutions:

**DDS Step 1.** Define DDS inputs:
- Neighborhood perturbation size parameter $r$ (given a default of 0.2)
- Maximum number of function evaluations, $m_{DDS}$
- Vectors of lower $x_{min}^D$ and upper $x_{max}^D$ bounds for all D decision variables
- Initial solution $x^0=[x_1, \ldots, x_D]$, drawn from list of $n_{beh}$ random initializations

**DDS Step 2.** Set counter $i$ to 1, evaluate objective function $F$ at initial solution, $F(x^0)$
- $F_{best}=F(x^0)$, and $x_{best}=x^0$

**DDS Step 3.** Randomly select $J$ of the $D$ decision variables for inclusion in neighborhood $\{N\}$
- Calculate probability each decision variable is included in $\{N\}$ as a function of the current iteration count: $P(i) = 1-ln(i)/ln(m_{DDS})$
- FOR $d=1, \ldots, D$ decision variables, add $d$ to $\{N\}$ with probability $P$
- IF $\{N\}$ empty, select one random $d$ for $\{N\}$

**DDS Step 4.** FOR $j=1, \ldots, J$ decision variables in $\{N\}$, perturb $x_{best}$ using a standard normal random variable, $N(0,1)$, reflecting at decision variable bounds if necessary, and scaled by the perturbation size parameter $r$:
- $x_{new}^j = x_{best}^j + \sigma^j N(0,1)$, where $\sigma^j = r (x_{max}^j - x_{min}^j)$
- IF $x_{new}^j < x_{min}^j$, reflect perturbation:
  - $x_{new}^j = x_{min}^j + (x_{min}^j - x_{new}^j)$
  - IF $x_{new}^j > x_{max}^j$, set $x_{new}^j = x_{min}^j$
- IF $x_{new}^j > x_{max}^j$, reflect perturbation:
  - $x_{new}^j = x_{max}^j - (x_{new}^j - x_{max}^j)$
  - IF $x_{new}^j < x_{min}^j$, set $x_{new}^j = x_{max}^j$

**DDS Step 5.** Evaluate $F(x_{new})$ and update current best solution if necessary:
- IF $F(x_{new}) \leq F_{best}$, update new best solution:
  - $F_{best}=F(x_{new})$ and $x_{best}=x_{new}$

**DDS Step 6.** Update iteration count $i = i+1$, and check stopping criterion:
- IF $i = m$, STOP, print output (e.g., $F_{best}$ and $x_{best}$)
- ELSE go to DDS Step 3.

**DDS-AU Step C:** Classify the $n_{beh}$ final best DDS solutions (one per trial) as behavioral or nonbehavioral based on pre-defined model acceptability threshold.

**DDS-AU Step D:** Consider possible outcome improvements:
- Give the best nonbehavioral solutions additional DDS optimization trials
- Ease the behavioral threshold
While there are a large number of potentially tunable parameters in the SVAT model developed in Chapter 3, this analysis will focus on eight parameters that govern key parts of the model, and which have less support from measurements taken at the field site. These parameters, their suggested initial values, and lower and upper bounds, are given in Table 4-2, and described in Chapter 3. There are inherent trade-offs when choosing the number and types of parameters to test in a sensitivity analysis. The parameter subset is held here to eight of many parameters in order to keep the analysis tractable, and follows much preliminary research into parameters seeming to govern flux estimates. In this study I focus on parameters that scale and shape the response of plant stomata and leaf pressure to various environmental conditions. The stomata and leaf water potential are critical indicators and regulators of plant responses to the diverse array of input conditions – air temperature and humidity, available energy, light, and carbon resources, and the state of the soil. Therefore, understanding the interactions and sensitivities of parameters governing these reactions will contribute to understanding how the model performs under different environmental conditions, and to attempts to reduce the number of parameters.

In addition to the scaling and shaping parameters whose physical meaning derives in their ability to describe plant responses to different environmental conditions, two physically measureable parameters are included in the parameter subset for this analysis. $L_A$ is incorporated into this method because it acts as the primary scaling factor for moving from the point to the field scale, and its value is difficult to measure with accuracy. Additionally, using field mean $L_A$ can introduce some bias due to the nonlinear response of GPP to $L_A$ (Duursma and Robinson, 2003; Medlyn et al., 2003). Allowing this parameter some flexibility may reduce this potential source of bias. Similarly, while estimates of $g_{p,max}$ are given in Chapter 3, there is enough uncertainty in their calculation to warrant further investigation through sensitivity analysis, particularly since $g_{p,max}$ is a candidate parameter for model parsimony.

Table 4-2: SVAT model parameters optimized in DDS/GLUE analysis. $L_A$ values are estimated according to the field-based method in Chapter 3, and then allowed to vary within a 20% window around this estimate. Example for DOYs 179-181 is provided here.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Initial Value</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Units</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>$D_x$</td>
<td>1.5</td>
<td>0.5</td>
<td>5-10</td>
<td>kPa</td>
<td>Reference VPD for $g_s$ response function $f(D)$</td>
</tr>
<tr>
<td>$a_1$</td>
<td>16.9</td>
<td>6.75</td>
<td>22.5</td>
<td></td>
<td>Slope of stomatal conductance of CO$_2$</td>
</tr>
<tr>
<td>$L_A$</td>
<td>0.77 (or Estimate)</td>
<td>0.68 (or 90% of Estimate)</td>
<td>0.85 (or 110% of Estimate)</td>
<td>m$^2$ m$^{-2}$</td>
<td>Currently based on LAI-2000 estimates</td>
</tr>
<tr>
<td>$g_{plant,max}$</td>
<td>0.082</td>
<td>0.053</td>
<td>0.225</td>
<td>$\mu$mol MPa$^{-1}$ s$^{-1}$</td>
<td>Maximal plant conductance</td>
</tr>
<tr>
<td>$s_f$</td>
<td>2</td>
<td>0.05</td>
<td>5</td>
<td></td>
<td>Curvature factor for $A_{vl}$</td>
</tr>
<tr>
<td>$\psi_f$</td>
<td>-1.56</td>
<td>-2.60</td>
<td>-0.91</td>
<td>MPa</td>
<td>Reference $\psi_f$ for $A_{vl}$</td>
</tr>
<tr>
<td>$c$</td>
<td>3.85</td>
<td>2.8</td>
<td>6.65</td>
<td></td>
<td>Shape factor for $g_p$ vulnerability curve</td>
</tr>
<tr>
<td>$d$</td>
<td>3.96</td>
<td>2.64</td>
<td>6.27</td>
<td>MPa</td>
<td>Reference $\psi_f$ for $g_p$ vulnerability curve</td>
</tr>
</tbody>
</table>

The DDS-UA scheme is run in several ways to test its efficacy and to provide different perspectives on parameter sensitivity. Initial results in Chapter 3 suggest there may be some parameter trade-offs depending on temperature conditions, where higher temperatures, with higher vapor pressure deficits, may require higher values of $D_x$, the reference VPD for the stomatal conductance ($g_s$) response function. The bulk of the DDS-UA scheme’s computational
demand comes in the time for objective function evaluation, which in this case means running the salinity SVAT model over the course of the time period of interest at half hourly intervals. To compare predicted model responses to different weather conditions, several versions of the GLUE model are investigated:

i) The GLUE model is run over three days separately (DOY 179, 180, 181 of 2009) with $n_{beh}=200$ and $m_{DDS}=200$, to reflect differences in model performance in relatively hot days (i.e., DOY 179) and other, more characteristic days (i.e., DOY 180, 181).

ii) The GLUE model is run with $n_{beh}=100$ and $m_{DDS}=200$, where the likelihood function uses a three-day aggregated RMSE of half-hourly ET and GPP values (again, for DOY 179-181).

In each of these model simulations, the DDS algorithm is driven by a simple likelihood measure:

$$ L(\Theta|Y) = RMSE_{GPP} + RMSE_{ET} $$ \[1\]

Where $L(\Theta|Y)$ is the likelihood measure for the parameter set of the $i^{th}$ iteration ($\Theta$) conditioned on the eddy covariance-derived observations ($Y$) of gross primary productivity (GPP) and evapotranspiration (ET). The RMSE terms indicate the root-mean-square error of GPP [$\mu$mol m$^{-2}$s$^{-1}$] and ET [mm day$^{-1}$]. Summing across different units is somewhat subjective, though since the absolute values are within a similar range, this approach seems reasonable. The balance between these two portions is considered in the analysis, and can demonstrate where parameter changes can improve one part of the model with and without a trade-off in another part of the model’s performance. In addition to discovering parameter sensitivity, the GLUE method acts as a parameterization routine, and so a better parameter set may be determined from the results. Each trial contains a ‘best’ parameter set, and here these are considered ‘behavioral’. All other trial iterations are considered “non-behavioral”, even if their performance is near to or better than other behavioral solutions, so that adjacent iterations in nearby portions of the parameter space do not unduly influence the characterization of parameter prediction bounds.

The parameters governing leaf pressure are the focus of the DDS-AU work described above, and having model iterations in different parts of the parameter space will provide a useful dataset from which to explore parameter interactions. Parameter interactions will be explored with the goal of reducing the overall number of parameters and to focus on parameters critical to dominant processes. Key functions governing these processes are reviewed here (from Chapter 3).

The plant conductance $g_p$ in terms of unit leaf is modeled as an S-shaped function of leaf water potential (Tyree and Sperry, 1989). The Weibull function is employed for this purpose (Sperry et al., 1998):

$$ g_p = g_{p_{max}} \exp \left[-\left(-\frac{\psi_1}{d}\right)^c\right] $$ \[2\]

The reduction of $A_n$ in water-stressed conditions follows Daly et al. (2004), where there are reductions from a well-watered potential photosynthesis (or stomatal conductance) based on a function $A_{\psi_1}(\psi_1)$:

$$ A_n = A - P - R_d = A_{\psi_1}(\psi_1) \times A_{\phi,c_1,T_1}(\phi, c_1, T_1) - R_d $$ \[3\]

The empirical logistic response function of Tuzet et al (2003) is used to depict the reduction to stomatal conductance at more negative leaf water potentials:
where \( s_f \) and \( \psi_f \) are parameters that depend on morphological adaptations in different species. The parameters of equation [2] interact with the parameters of equation [4] in the connection between evapotranspiration and photosynthesis found in stomatal conductance. Changes in plant conductance directly influence the evapotranspiration rate predicted through the water flux method. These interactions will be explored using the set of iterations evaluated in the DDS-AU trials.

### 4.2.2 Salinity simulations: Parameterizing the Penman-Monteith Equation

In order to determine the effects of osmotic pressure on the Penman-Monteith-derived transpiration, when we set the two transpiration terms equal to each other, we can inversely determine \( \alpha \) and \( \beta \) type stresses as follows:

\[
E_{Type\,1} = f_{\text{PM}}(\alpha g_s) \tag{5}
\]

\[
E_{Type\,1} = E^{\text{PM}} = \beta f_{\text{PM}}(g_s) \tag{6}
\]

where \( f_{\text{PM}} \) is the Penman-Monteith equation expressed as a function of stomatal conductance, and \( E^{\text{PM}} \) is the Penman-Monteith transpiration with no osmotic effects. The \( \alpha \) term is comparable to one of the multiplicative environmental factors that reduce a maximal stomatal conductance, as suggested by (Jarvis, 1976), and commonly used in land surface models (Noilhan and Planton, 1989). The \( \beta \) term is comparable to the representation of drought-induced reductions to potential evapotranspiration in point-scale ecohydrological models (Laio et al., 2001; Rodriguez-Iturbe et al., 1999), and is widely used in “Type II” representations of saline stress (Cardon and Letey, 1992; Ragab et al., 2005). These stress-induced reductions can also be applied to an unstressed gross carbon assimilation rate (Cox et al., 1998), to mesophyll conductance (Calvet et al., 1998), and need not be linear (Ronda et al., 2001).

These interactions will be explored by driving the model using a prescribed range of salinity conditions [\( EC_{\text{solution}} \sim 0-25 \text{ dS m}^{-1} \)] that may be expected in a natural or a managed environment. The model is re-evaluated for the 2009 input period explored in Chapter 3 for salinity values throughout this range of values so that the effects of salinity concentrations can be evaluated under different time scales.

### 4.2.3 Modeling plant responses to climatic change under saline soil conditions

As a rough sensitivity analysis to test model performance under different environmental conditions, expectations related to climate change are applied to the parameterized SVAT model in two steps. First, the model’s sensitivity to separate changes in temperature and \( CO_2 \) concentration are considered. These cases are evaluated by assuming \( CO_2 \) levels of 390, 450 and 500 ppm for an eighty day period of 2009, holding all driving parameters constant except for air temperature. Temperature is first held to 2009 levels to explore the sole effect of \( CO_2 \) changes, and then is increased by 2°C, to test the interacting or compensating effects of \( CO_2 \) and temperature. This approach is similar to the constant fraction analysis, where changes in model output following a change from model input allows an exploration of model sensitivity. While
less comprehensive than the GLUE or Bayesian methods described earlier, this routine is
common in explorations of sensitivity to environmental conditions (Williams et al., 1998).

Second, specific climate change scenarios are loaded into the SVAT model to explore
interacting sensitivity to these inputs. A summary of model scenarios considered for this
analysis is provided in Table 4-3, and is derived from Cayan et al (2008b), who use the IPCC
Fourth Assessment simulations of twenty-first century climates under B1 (low emissions) and
A2 (medium-high emissions) scenarios. These researchers downscale results from two climate
models: the Parallel Climate Model (PCM1, from NCAR and DOE) and the NOAA Geophysical
Fluid Dynamics Laboratory CM2.1 model (GFDL). This downscaling parses global climate
model results to finer scales that account for California’s complex topographical landscape, a
difference that is especially important for representing changes to snow accumulation. Since the
PCM has a relatively low sensitivity to projected greenhouse gas forcing, and the GFDL model
has a relatively high sensitivity, the PCM B1 scenario and the GFDL A2 scenario together
provide a useful envelope to characterize future climate possibilities. These predicted
temperature increases agree with past studies (VanRheenen et al., 2004) of climate model
downscaling in California’s Bay-Delta region, which anticipate increases of average air
temperatures by 0.5, 1.2, and 1.9 °C by the periods 2010-2039; 2040-2069; and 2070-2098,
respectively.

Table 4-3: Climate change scenarios considered for analysis; temperature increases over historical mean from GFDL and
PCM B1 and A2 simulations, downscaled for Northern California (Cayan et al., 2008b); CO₂ predictions from IPCC
Fourth Assessment emission scenarios (Meehl et al., 2007).

<table>
<thead>
<tr>
<th></th>
<th>Temperature</th>
<th>2030</th>
<th>2050</th>
<th>2090</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean (1961-1990)</td>
<td>PCM</td>
<td>PCM</td>
<td>PCM</td>
</tr>
<tr>
<td></td>
<td>GFDL</td>
<td>B1</td>
<td>A2</td>
<td>B1</td>
</tr>
<tr>
<td>Annual °C</td>
<td>9.3</td>
<td>8</td>
<td>0.5</td>
<td>1.5</td>
</tr>
<tr>
<td>Summer °C (JJA)</td>
<td>21.5</td>
<td>17.9</td>
<td>0.6</td>
<td>2.1</td>
</tr>
<tr>
<td>Winter °C (DJF)</td>
<td>-0.46</td>
<td>0.08</td>
<td>0.7</td>
<td>1.4</td>
</tr>
<tr>
<td>Atmospheric CO₂ [ppm]</td>
<td>390</td>
<td>433</td>
<td>453</td>
<td>490</td>
</tr>
</tbody>
</table>

These climate scenarios are evaluated using meteorological and plant data from 2008 and
2009, where the air temperature and CO₂ concentrations conditions are adjusted according to
Table 4-3 (and time of year). Changes in precipitation are ignored to keep the focus of this study
on summer-time changes in climate, and to reflect that the dominant driver of soil moisture at the
field site is based on management controls on irrigation and pumping. This simulation is
relatively simple in that it does not propose a change in plant growth or LAI through the season,
nor does it model any changes to salinity levels or water availability. Additionally, leaf
downregulation of photosynthesis is not incorporated into model predictions. This well-studied
phenomenon occurs as a reduction in the response of leaves to CO₂ through acclimation to
higher ambient CO₂ concentrations, and is supported by Free-Air CO₂ Enrichment (FACE)
experiments (Ainsworth and Long, 2005; Arora et al., 2009). Such studies also suggest an
increase in CO₂ will encourage plant water use efficiency and light use efficiency, and will
reduce stomatal conductance and transpiration. The model used in this analysis does not impose
additional down-regulatory behavior, and so these scenarios should be seen as offering guidance
towards assessing the sensitivity of the model to changed environmental inputs (as opposed to
changes in parameterization suggested earlier). This modeling has the additional benefit of
suggesting how to explore responses of the landscape and plants to salinity under different climate scenarios.

4.3 Results

4.3.1 GLUE DDS-AU results

The GLUE-based DDS-AU algorithm was run on the SVAT model presented in Chapter 3 for three separate calendar days, to search for 200 behavioral parameter sets minimizing half-hourly errors in water and carbon fluxes for each day. The search for these 200 targeted behavioral parameter sets \(n_{beh}\) involved 200 model evaluations \(m_{DDS}\) per DDS optimization trial. A further search for 100 targeted behavioral parameter sets with 200 model evaluations was performed for the three-day period taken together.

GLUE results are traditionally reported as scatter plots of parameter values against model efficiency, and then cumulative distribution function plots which compare behavioral and non-behavioral model iterations. This presentation style is in Figure 4-1 for parameter \(D_s\), and in Appendix A for the other seven parameters analyzed in the GLUE framework. Parameters are plotted against the likelihood function, its two constituent parts (RMSE\(_{ET}\) and RMSE\(_{GPP}\)), and modeled leaf water potential. These figures also present DDS-AU trial information (such as initial parameter values, parameter bounds, and best-fit parameter values). Finally, these figures present the cumulative distribution of behavioral parameter sets (which are the best outcome-generating parameters for each DDS-AU trial). These cumulative distributions are compared to all parameter guesses throughout the DDS-AU trials. Results are further summarized in Figure 4-2, which contains boxplots of behavioral and non-behavioral parameters for each of the GLUE models, and for each component of the likelihood function. In each case, results are presented for each day separately, as well as the combined three-day trials.

Key responses of modeled fluxes (ET and GPP) to the parameters are described here, with an eye towards reducing model error over both the short and long term and in increasing understanding of field or leaf-scale physical processes. The parameter \(D_s\), controlling stomatal responses to vapor pressure deficit, tends to have a greater influence on ET than on GPP. Changes in \(D_s\) can influence model performance in opposite directions: raising \(D_s\) lowers RMSE\(_{GPP}\) but raises RMSE\(_{ET}\). This response is consistent with results in Chapter 2 and Chapter 3, which demonstrate that pepperweed can photosynthesize under higher vapor pressure deficits than traditional models predict. There are diminishing returns to increasing \(D_s\) beyond values of \(D\) found at the field site.

Results from two parameter pairs demonstrate the concept of equifinality as applied to this model. First, through their competing influences on \(g_s\), the parameters \(D_s\) and \(a_j\) are inversely correlated with \(r^2=0.68\), evaluated through the set of behavioral solutions of the three-day trial. Second, the maximum plant conductance \(g_{p,max}\) is positively correlated with \(s_f\) \(r^2=0.52\) for the three-day trial’s behavioral set). These parameters set clear controls on estimated leaf water potential (Figure A-3 and Figure A-4). Higher \(s_f\) values create steeper stomatal responses to leaf pressure and tend to reduce variation in daily minimum leaf pressure. Higher \(g_{p,max}\) values increase plant conductance, and reduce restrictions on water flow through the xylem. Therefore, these parameters each act to compensate the other’s influence on plant water flux, and seem to be more influential in determining modeled leaf pressure estimates than similar changes in \(c\), \(d\), and \(\psi_f\), the other scaling and shape parameters governing plant responses to leaf pressure.

This set of parameters governing plant responses to leaf pressure controls both the magnitude of leaf pressure estimates and the responses of flux estimates to that value of leaf
pressure. For instance, while it is clear that high values of $c$ (Figure A-6) and $d$ (Figure A-7) act to reduce leaf water potential estimates, they have a comparatively smaller effect on model fitness than $\psi_f$ (Figure A-5), whose value seems largely responsible for overall model fitness. Field estimates of mid-day leaf pressure during the middle of the growing season were presented in Chapter 3, with median afternoon water potential ranging from -1.3 to -2.24 MPa. This field-based constraint may push parameter selection towards models that generate lower leaf water potential without sacrificing model fitness.

![Figure 4-1: Response of model efficiency to $D$ parameter for three days. Plots show (left to right) the response of the likelihood measure, its constituent parts (RMSE$_{ET}$ and RMSE$_{GPP}$), and $\psi_f$ to changes in parameter value. DDS-AU optimization information is presented to demonstrate trial inputs (initial conditions in red; lower and upper bounds in blue) and each trial’s best value (in green). Cumulative likelihood distribution of behavioral (best of each DDS-AU trial) and nonbehavioral parameters are provided. Behavioral sets for ET and GPP measures are the best 50% of overall behavioral sets, as measured by RMSE$_{ET}$ and RMSE$_{GPP}$, respectively. Legend term ‘m’ is the median value for behavioral...](image)
or non-behavioral parameter sets, as indicated. From top to bottom, the plots show results for GLUE models assessing performance for DOY 179, 180, 181, and for the performance across combined DOY 179-181.

Figure 4-2: Linearly scaled behavioral (blue) and nonbehavioral (red) parameter values represented as boxplots for DDS-AU simulations. Simulations for three days pooled together have wider boxes; simulations for three days evaluated separately have narrower boxes in chronological order (DOY 179, 180, 181) to the left (behavioral) and right (nonbehavioral) of the pooled simulation data. From top to bottom, results demonstrate parameter effects on the GPP fit, the ET fit, and the combined fit, which is the model’s likelihood function. Each box has bounds at the lower and upper quartile, with the interior line drawn at the median value, and whiskers contain the most extreme values within 1.5 times the interquartile range. Outliers are marked with a point. The width of median notches are determined so that box plots whose notches do not overlap have different medians at the 5% significance level, assuming a normal distribution.

The best fit model results from the DDS-AU parameter sets from each day are compared to the best fit model result from the combined set of days; each of these models are then compared to the eddy covariance-derived data Figure 4-3. The range of behavioral parameter sets derived from this analysis generally cover the natural variability in flux estimates from eddy covariance (which seem uncorrelated with incoming environmental conditions), although GPP estimates in the hotter day (DOY 179) still underestimate measured values. The behavioral
models from the three-day GLUE analysis tend to fit most closely the ‘average weather’ day (181), and reduce the goodness of fit to the hot day (179).

Figure 4-3: Comparison of best model results to eddy covariance derived data. Black lines represent eddy covariance-derived data; red, green, and light blue lines represent the 200 best modeled results for each DDS-AU run of the one-day optimization trials, and the purple lines represent the bounds of the 100 best modeled results from the three-day optimization trials.

4.3.2 Salinity sensitivity
The sensitivity of the model outputs to salinity levels is analyzed using the best-guess parameter values from the combined three-day parameterization in section 4.3.1 (Table 4-4). The model is run with these parameters over a range of salinity values thought common in environmental systems to test how changes in osmotic potential will modify water and carbon flux rates. Half-hourly average reductions in evapotranspiration and photosynthesis show linear responses to increased salinity (Figure 4-4). Responses to salinity in this model are nearly always linear ($r^2 > 0.99$). Stomatal responses to salinity drive nearly identical responses in carbon uptake, and tend to be stronger than responses in evapotranspiration. In other words, the plant becomes less water-use efficient under increasing salinity stress, as it must release more water for proportionally less carbon gained. While responses in GPP tend to be stronger than in ET (i.e., have a steeper slope), the ET response is more variable in reaction to changing environmental conditions through the growing season (Figure 4-5).
Table 4-4: Best parameter set from combined three-day GLUE analysis (used for salinity and climate change scenarios).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Best GLUE value</th>
<th>Units</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>$D_x$</td>
<td>3.31</td>
<td>kPa</td>
<td>Reference VPD for $g_s$ response function $f(D)$</td>
</tr>
<tr>
<td>$a_1$</td>
<td>13.7</td>
<td></td>
<td>Slope of stomatal conductance of CO$_2$</td>
</tr>
<tr>
<td>$L_{AI}$</td>
<td>93% of Licor-2000 Estimate</td>
<td>m$^2$ m$^{-2}$</td>
<td>Currently based on Licor-2000 estimates</td>
</tr>
<tr>
<td>$g_{plant,max}$</td>
<td>0.178</td>
<td>$\mu$mol MPa$^{-1}$ s$^{-1}$</td>
<td>Maximal plant conductance</td>
</tr>
<tr>
<td>$s_f$</td>
<td>1.88</td>
<td></td>
<td>Curvature factor for $A_{vpd}$</td>
</tr>
<tr>
<td>$\psi_l$</td>
<td>-0.936</td>
<td>MPa</td>
<td>Reference $\psi_l$ for $A_{vpd}$</td>
</tr>
<tr>
<td>$c$</td>
<td>4.17</td>
<td></td>
<td>Shape factor for $g_p$ vulnerability curve</td>
</tr>
<tr>
<td>$d$</td>
<td>4.57</td>
<td>MPa</td>
<td>Reference $\psi_l$ for $g_p$ vulnerability curve</td>
</tr>
</tbody>
</table>

Figure 4-4: Seasonal half-hour average responses of fluxes and stomatal conductance to salinity, relative to values derived with no salinity imposed to the system. The slope of each line is provided in the legend.

Figure 4-5: Time series of response to salinity (2009).
The response of plant fluxes to salinity tends to be stronger under dryer soil conditions and higher air temperatures (or vapor pressure deficits), when conditions may already be primed for stress (Figure 4-6). The correlation between air temperature and vapor pressure deficit is hard to separate in this analysis, and may depend on the parameters chosen by the GLUE analysis (i.e., $D_x$ and $a_I$). Changes correlated to PAR or $[R_n-G]$ may be residual from the correlation of these parameters with time of year, and may change in sync with seasonal changes in soil moisture. Soil moisture conditions seem to be the dominant driver of the response to salinity.

![Figure 4-6: Response of fluxes to salinity plotted against input variables. Correlations between the input variables and the response of GPP and ET fluxes are provided as $r^2$ values in each subplot.](image)

### 4.3.3 Climate model results

The modeled responses to temperature and CO$_2$ perturbations suggest a more water-efficient land cover, with reduced evapotranspiration rates and increased carbon uptake in each perturbation. Responses of the perturbations to CO$_2$ and temperature are presented in Figure 4-7. In general, it appears that changes in temperature are more important in controlling transpiration, while in near-present levels of CO$_2$ (i.e., 450 ppm), there is some resilience to temperature-driven increases in GPP. The effect of increased temperature on CO$_2$ uptake is harder to qualify: GPP is higher at either 390 ppm or 500 ppm than at 450 ppm. While in each case GPP is slightly higher than in present conditions, the increase in GPP is less striking than the reduction in evapotranspiration.
Figure 4-7: Time series of ET and GPP in T and [CO₂] perturbations, compared to eddy covariance estimates and model results assuming current climate conditions. Perturbation scenarios to input variables hold other environmental variables constant. 2009 model CO₂ levels are based on measurements so have some diurnal change, but have a mean value of 370 ppm for this period (standard deviation 17.6 ppm).

A more water-efficient landscape is also apparent in the high-CO₂, high-temperature case predicted for 2090 (GFDL A2 scenario), where nearly 40% more photosynthesis is achieved using 40% less water, relative to present conditions (for the 80 day period presented in Figure 4-8). The results highlight the increasing divergence between the climate scenarios considered: results from 2090 in the more conservative PCM projection resemble results from 2050 in the more intense GFDL projection. Since these two cases apply similar CO₂ concentrations (536 and 530, respectively) but the temperature increases differ more substantively (1.6 and 3.4°C, respectively), the relatively contribution of these changes can be inferred. Photosynthesis is nearly identical in the two cases (both predict 309 gC m⁻² of GPP during the period studied), but the conservative 2090 model predicts less evapotranspiration. These results support the suggestion that effect of higher temperature is more responsible for reductions in water use efficiency via increased transpiration than in decreased uptake: the plant can take up the same carbon, but at a greater cost.
Figure 4-8: Time series of predicted fluxes for climate change scenarios (compared to eddy covariance estimates and model results assuming current climate conditions).

Changed sensitivity of water and carbon fluxes to salinity is less clear in the climate change scenarios (Figure 4-9), and may be mediated by a more complex mix of environmental and parameter conditions than investigated here. Generally, the response to salinity under the future climate projections is similar to responses to salinity in the present day, and GPP is consistently more responsive to salinity than ET. The role of salinity in governing these fluxes is less important than changes in temperature or CO₂ concentration.

Figure 4-9: Time series of flux response to salinity for climate change scenarios.

4.4 Discussion
4.4.1 Discussion of DDS and GLUE results
Several drawbacks of the DDS-AU scheme are mentioned by its authors and warrant attention here. The DDS-AU approach loses some ability to ensure that solutions are found throughout the behavioral parameter space when iterations are seeded from the same initial values, and when
each iteration is only slightly distinct from the current best-fit solution. The model is a so-called ‘greedy’ algorithm in that it never accepts as the current solution any inferior parameter set than that which generates the best likelihood, and so may be more likely trapped within local optima, though this concern is alleviated to some extent by the variable size of the neighborhood-oriented search. Additionally, both the GLUE approach itself and the DDS-oriented modifications of it depend on some subjective approaches to the model’s fitness evaluation, and on its own model parameters (i.e., $n_{neh}$ and $m_{DDS}$). These concerns should be considered when interpreting the results presented here, though still the algorithm has the ability to find competing optimal solutions, identify crucial parameters, and guide model improvements. The heuristic modification of the DDS search algorithm – keeping a focus on the parameters whose changes reduce the likelihood function – should be evaluated in more detail before offered as a definitive improvement to the method, though may enable fewer function iterations.

The sensitivity analysis shows that $D_\chi$ for pepperweed may be higher than other species modeled in the literature. The diminishing returns achieved in response to increasing its value beyond 5-6 kPa suggest that a different type of model could be considered. The field site is situated very near to the Sacramento River and receives winds that pass over the River and Delta, so relative humidity is generally greater than 50%. This circumstance, as well as pepperweed’s tolerance to dry conditions, may make pepperweed more capable of taking up carbon in the relatively high vapor deficits found on hotter days.

Model simplification is an important goal for considering locations offering less data to drive and evaluate model performance. The correlations between parameter pairs $a_\chi$-$D_\chi$ and $g_{p,max}$-$s_f$ offer a good starting point to reduce the scope of model parameterization. Leaf-level characterization of stomatal or photosynthesis responses to humidity may reduce equifinality by constraining the $a_\chi$ and $D_\chi$ parameters. Better field or lab estimates of plant conductance and $g_{p,max}$ allow $s_f$ to be constrained. Consistency (or not) in mid-day leaf water potential estimates further constrains estimates of $c$, $d$, and $\psi_f$, as well as $g_{p,max}$ and $s_f$.

### 4.4.2 Discussion of salinity sensitivity

Modeled effects of soil salinity show linear reductions to evapotranspiration, net photosynthesis, stomatal conductance, and leaf water potential for any half-hourly timer period. This linear response appears in agreement with many models of salinity which assume linear or threshold-linear responses to soil salinity levels (Katerji et al., 2003). Qadir et al (2000) provide a useful table listing seasonal yield-based salt tolerance parameters, where yield is reduced once salinity is increased beyond a threshold (ranging from $EC_e$ 0.9-11.4 dS m$^{-1}$) with slopes ranging from 2.5 to 33 % per dS m$^{-1}$, where $EC_e$ is the average electrical conductivity of the saturated soil paste extract of the root zone. Broad differences between genotypes within a species, between environmental conditions during growth, and especially between species are evident (Eynard et al., 2005). Modeled results in this chapter indicate that pepperweed may respond on the lower end of these species, which fits its prior characterization as a moderate halophyte. An important caveat is that modeling changes in response to salinity are not validated by field data, which is taken under relatively uniform salinity conditions. The fitness of pepperweed comes in part from its higher ability to take up carbon (in $V_{c,max}$ and $J_{max}$) in high temperatures (i.e., $H_a$ for $V_{c,max}$; $H_a$ for $J_{max}$), and its ability to photosynthesize in high vapor pressure deficits.

The linear seasonal response to salinity has been modified in recent years by many who view nonlinear, often sigmoid-shaped, responses as better descriptions of plant stress (Feng et al., 2003; Steppuhn et al., 2005a; Steppuhn et al., 2005b), though both are common (Bauer-
Gottwein et al., 2008). Responses of water and carbon fluxes modeled in this work are linear or mostly linear within most time-frames used, though different slopes during different environmental conditions cast doubt on the expectation that a single slope can be used with confidence across a whole season, particularly for environments where atmospheric or soil conditions are not constant. The use of seasonal response functions that relate yield reductions to evapotranspiration reductions is common, and supported by some past research (Ben-Gal et al., 2003), though other researchers have found higher-than-predicted yields (Ferrer-Alegre and Stockle, 1999). Findings here indicate that salinity effects can change water use efficiency, so may provoke questions about whether crop yields (or plant growth) under stress are simple linear reductions of maximal, unstressed yields.

The modeled results support either $\alpha$ or $\beta$ formulations of salinity stress (equations [5] and [6]) in that both stomatal conductance and evapotranspiration have nearly linear responses to soil osmotic potential. The stomatal conductance response is practically identical to the response of GPP, and so may be useful to those considering carbon flux dynamics more than water resources. Both models though show non-linear responses to other environmental conditions, so providing stress as a multiplicative function applied to either a Penman-Monteith estimate of evapotranspiration or to a Jarvis-type estimate of stomatal conductance may cause inaccurate flux estimates in varying environmental conditions. Leaf-level research has elsewhere supported the notion that stomatal and mesophyll conductance are reduced in saline conditions (Bongi and Loreto, 1989; Loreto et al., 2003), so an interesting extension to this work would incorporate an analysis of mesophyll conductance. Further work could also include investigating sensitivity to a larger range of environmental conditions than exists during the time period covered by this modeling exercise. The findings of this chapter demonstrate that the response to salinity may be greater under conditions where the plant is already nearer to stressed conditions—whether in lower soil moisture conditions or higher vapor pressure deficits.

4.4.3 Discussion of implications for climate change
This chapter presents relatively simple modeled results for the plant water use and carbon uptake of pepperweed in saline soils under a variety of expected future climate conditions. This analysis does not consider changes to plant growth rates, nor does it rely on predictions of adaptations to these climate conditions. The model’s focus on the physiological aspects of water flux, and how they influence carbon uptake through stomatal controls may be insufficient to capture the full range of responses to climate change. Changes in the system’s response to salinity in different climate scenarios is slight; of much greater interest are changes to the fluxes themselves in different climates. The reduction in water use (and increase in productivity) may have the benefit of reducing salt loads to the roots, xylem, and leaves (Maggio et al., 2002). These ideas suggest that a greater range of processes should be considered in order to define how pepperweed in this landscape may respond to projected climate changes. Under the current modeling framework, results suggest that in higher CO$_2$ environments, increases in temperature will reduce transpiration more than relative increases in GPP. These results suggest that stomatal responses to higher vapor pressure deficits may be more important to evapotranspiration than expected temperature-induced increases to the carboxylation parameters ($V_{c,max}$ and $J_{max}$) are to photosynthesis.

There are many unknown considerations for modeling future climates generally and at this site in particular. The salinity-SVAT model already does not perform as well on hotter days, and so may underpredict the ability of pepperweed to take advantage of hotter, CO$_2$ enriched
environments. The ability of pepperweed to withstand a variety of future climate changes bears ill for land managers and ecologists concerned with its spread through native ecological zones and in agriculturally significant areas. This result holds regardless of the caveats mentioned about model predictability in future climates. The model is able to investigate the role of changed conditions on water use efficiency, and in combination with earlier leaf-level evidence, suggests that pepperweed is situated both presently and in the future to extract available resources from its environment. Future work should consider how to scale these predictions throughout California’s Delta Region, which is the subject of great management interest for its regional water resources and economic importance.
4.5 Works Cited
Cayan, D. et al., 2008a. Climate change projections of sea level extremes along the California coast. Climatic Change, 87(0): 57-73.


Appendix A. Additional DDS-AU Parameter Results

Additional results from the DDS-AU modeling section are provided in this appendix. In the style of Figure 4-1, assessments of model sensitivity to individual parameters are shown in the following seven figures. Each contains scatter plots, model information, and cumulative distribution functions for the GLUE simulations (for DOY 179, 180, and 181 separately, and also for the combined three-day simulation).

Figure A-1: Model sensitivity to parameter $a_i$ (similar interpretation to Figure 4-1).
Figure A-2: Model sensitivity to $L_A$ estimate (similar interpretation to Figure 4-1).
Figure A-3: Model sensitivity to $S_{\text{plant, max}}$ value (similar interpretation to Figure 4-1).
Figure A-4: Model sensitivity to $s_f$ parameter (similar interpretation to Figure 4-1).
Figure A-5: Model sensitivity to $\psi$ parameter (similar interpretation to Figure 4-1).
Figure A-6: Model sensitivity to $c$ parameter (similar interpretation to Figure 4.1); note that parameter bounds are changed for some iterations, DOY 179.
Figure A-7: Model sensitivity to $\alpha$ parameter (similar interpretation to Figure 4-1); note that parameter bounds are changed for some iterations, DOY 179.
Chapter 5 Summary and Conclusions

5.1 Conclusions
In this dissertation I develop, evaluate, and test a model of plant evapotranspiration and carbon uptake in the context of a saline soil environment, and drive the model using leaf physiological parameters determined from field measurements. This model expands current representations of soil salinity by incorporating them into a soil-vegetation-atmosphere transfer model that includes descriptions of leaf-atmosphere interactions. In addition to improving the framework of investigation for questions relating to the effects of soil salinity on root water uptake and leaf carbon assimilation, the specific case study used should progress understanding of perennial pepperweed, an invasive species prevalent in an ecologically and agriculturally important region of California. The research work in this dissertation starts at the leaf scale (Chapter 2), where the responses of pepperweed leaves to changes in environmental conditions are quantified. In Chapter 3, the research focus moves towards the scale of the plant and the field in which it resides, as soil-root, plant body, and leaf-atmosphere interactions are integrated into a single model. This single-plant focus is scaled to represent field-level processes through the leaf area index, whose measurement uncertainty and adequacy as a parameter are discussed. In Chapter 4, I prepare the way for approaching salinity questions at the regional scale by investigating the sensitivity of the model to a subset of its parameters. This analysis also helps characterize the water use efficiency of pepperweed, its resilience to climate change, and its ability to take advantage of high temperatures despite high vapor pressure deficits. These achievements are expanded upon here, and then suggestions and guidelines for future research are provided.

Field measurements detailed in Chapter 2 provide expanded understanding of pepperweed’s characterization and success as an invasive species. Pepperweed has a high leaf nitrogen content, which both allows for a highly active photosynthetic apparatus and provides evidence of its ability to take advantage of its environmental surroundings. The high rates of carbon or light limited photosynthesis, $V_{c,\text{max}}$ and $J_{\text{max}}$, encourage carbon uptake, and the lack of apparent deactivation at high temperatures helps distinguish pepperweed from more sensitive species. These parameter estimates are a starting point; measurements are taken over a broad range of field and environmental conditions, and so represent field-average conditions, and as a result may be difficult to scale beyond this research site or into different environmental conditions. A possible adaptation to drought, temperature, or saline stress may be exist in the difficulty to uncover evidence of internal resistances to carbon assimilation, though questions about modeling and measurement accuracy preclude ruling out the influence of this resistance. Taken together, the characterization of pepperweed’s photosynthetic machinery indicates an aggressive invasive species, whose success in spreading through different ecological and agricultural settings may derive in part from its high capacity to take advantage of local resources.

The model presented in Chapter 3 is capable of characterizing the role of soil osmotic potential on leaf-level gas exchange and field-level fluxes. The model’s approach builds on process-focused models of plant water flux that incorporate different interactive effects of various environmental variables. Its ability to distinguish between sunlit and shaded portions of the plant canopy will be of particular use when modeling is extended to investigate unmowed, near-riparian patches of pepperweed, where LAI values can be as high as 5.03 (DOY 134, 2009), rather than the field average (maximum mean value 0.82, DOY 174, 2009; maximum point value 3.83, DOY 140, 2009). Results presented in Chapter 3 demonstrate both the difficulty in
adequately assessing the leaf area index and the importance of this parameter. Despite problems in assessing field average LAI over the course of the year, in part due to photosynthetically active leaf material below the measurement height of the LAI-2000, the model performs well during the peak of the growing season, and is able to capture both evaporative and carbon fluxes at the diurnal scale.

Results in Chapter 4 build on lessons from the leaf parameter sensitivity analysis presented in Chapter 2. In each case, numerical interactions between parameters and within models are considered. Sensitivity analysis is used to encourage model parsimony through parameter or process reduction. Model parsimony is a difficult goal when considering multiple, often competing, processes that determine a key physiological state, such as stomatal conductance. The SVAT model merges representations of the effects of leaf water potential into the descriptions of both stomatal conductance and photosynthesis; it also incorporates the slope term $a_1$ and the function $f(D)$ of vapor pressure deficit. In a hot environment with a dry upper soil layer and a salt affected saturated zone, there are interactions in the competing controls of stomatal conductance. In the sensitivity analysis of parameter interactions, I identify two pairs of parameters which may be set as functions of each other, reducing the number of overall free parameters. The analysis also clarifies the importance of field measurements to constrain midday leaf potential values and the whole-plant conductance.

Anticipated implications of climate change are predicted; most importantly, pepperweed should increase its carbon uptake and release less water in high temperature, high CO$_2$ environments. Agricultural and ecological models depend on accurate and predictive understanding of plant growth, rates of photosynthesis and transpiration, and the role of environmental stresses in moderating those rates. Water use efficiency is of special interest in an increasingly water-scarce world. The role that irrigation plays in controlling water use and in encouraging water efficiency is both important and controversial (Ward and Pulido-Velazquez, 2008). Past studies have described how stresses on plant behavior, and subsequent reductions in transpiration, have larger-scale effects on watershed hydrology through changes in surface runoff (Felzer et al., 2009). It is expected then, that a more efficient landscape may encourage changes in irrigation and pumping requirements, and should be incorporated into predictions of water resources in California.

This work should be useful to water resources planners in several ways. First, it provides a baseline of support for predicting water and carbon fluxes resulting from changes in delta land use patterns. By more greatly understanding plant responses to salinity, it can help constrain estimates of the partition between plant and microbial responsibility for carbon fluxes (both carbon dioxide and methane). Second, it helps validate modeling efforts at the project’s research site by more accurately describing the plant community’s response to changing soil conditions. A consequence of this improved modeling will be enhanced relevance of the larger study throughout the delta region. Third, modeling results from this work will be general enough to have applications in other parts of California and elsewhere that suffer from salt-degraded soils. Through its use of high quality near-continuous flux data in a saline environment these research results provide an opportunity for increasing the temporal resolution of models that consider plant responses to salt stresses.

5.2 Future research

Coupling the model presented here with a simulation of crop yield or plant growth could provide a powerful depiction of the effects of salts on the evaporative flow of water through the
environment. These fluxes are of importance to water resources managers, climatologists, land use planners, and downstream users of irrigation water. A precise and crop specific model would allow for careful projections of irrigation needs, accounting for the tolerance of crops to different levels of salinity, and their different physiological capabilities with regard leaf water potential. These coupled models will allow for predictive as well as analytical descriptions of how much irrigation is needed to counteract the effect of soil salinity. These models should complement the work of plant geneticists (Tester and Bacic, 2005) working towards increasing plant tolerance to drought and salinity stress by quantifying the implications of reaching various tolerance targets.

The relevance of this modeling framework will be enhanced through upscaling to support landscape to regional analysis of areas affected by soil salinity. A possible scheme for this upscaling is to incorporate the soil’s osmotic potential into pedo-transfer functions. Because the soil’s osmotic potential depends on its water content as well as its salt concentration, and because the water content also controls soil matric pressure, relatively simple modifications to existing pedotransfer functions within land surface models may expand the relevance of these models to salinized landscapes. Groenevelt et al (2004) describe interactions between soil moisture content and osmotic potential, and offer a useful starting point for this type of analysis. There is increased interest in increasing the physiological relevance of larger-scale models. Recent efforts have demonstrated that photosynthesis-based SVAT models can be incorporated into land surface and atmospheric boundary layer schemes (Garcia-Quijano and Barros, 2005; Niyogi et al., 2009). Further expansion of these models to consider salinity effects would benefit understanding of agricultural regions and areas where seawater intrusion into the groundwater is changing ecological productivity.

This research suggestion also points to the need for improved measurement techniques to characterize soil water content and its influence on matric and osmotic potentials, which depend on soil type and history. The importance of soil moisture in governing the response of plants to salinity is evident in the model results presented in Chapter 4, where I demonstrate that plant responses to salinity are heightened under more arid soil conditions. In even dryer environments, the interactions between drought and salinity stresses may be increasingly important. In this research site, pumping and irrigation decisions are important determinants of how plants will respond to the salt in their environment.

The results presented in this dissertation hint towards the need for better understanding of numerically-derived errors in parameter estimation. The standard methods for characterizing key photosynthetic parameters involve fitting four or more parameters to a non-rectangular parabolic relationship between carbon uptake and light or CO₂, where dominant limitations change in response to temperature, humidity, or physiological conditions. Moreover, the measurement series itself can modify leaf responses to the conditions being studied, and the time of the measurement sequence can span changes in external environmental conditions. In Chapter 2 I reject as currently inoperable an attempt to determine daytime respiration and the photo-compensation point through fitting non-rectangular hyperbolae as too numerically challenging. The optimization routines attempted are too sensitive to initial conditions and local minima for a satisfactory characterization of the photosynthetic parameters. These numerical questions are increasingly a focus of research (Dubois et al., 2007; Ethier and Livingston, 2004; Miao et al., 2009; Patrick et al., 2009; Su et al., 2009), and could be expanded further using some of the methods considered in this dissertation.

The SVAT model should likewise be investigated to discover acceptable uncertainties on the parameters determined from the photosynthetic investigations. Then, the photosynthesis
models can be tested to suggest a new measurement routine – with more or differently-spaced increments of light or CO₂, under different ranges of measurement error. Additionally, the importance of uncertainties in mesophyll resistance, stoichiometric ratios, and cuticular conductance can be addressed in relation to overall fluxes, and relative to other determinants, such as SVAT model parameters, LAI, and environmental conditions.

The role of agriculture in discussions of water resources usage and in the global carbon cycle is significant. The effects of agricultural land use are important, and often underestimated for determining the global carbon budget – the role of individual pastur lands in particular can vary from being a net carbon sink to a net carbon source (Shevliakova et al., 2009). The model developed in Chapter 3 can be extended to incorporate land management recommendations to predict how to create a carbon sink in an already managed environment, and so has broad implications in land-oriented responses to the threat of climate change.
5.3 Works cited