

**Savannas and seasonal drought:
The landscape-leaf connection through optimal stomatal control**

by

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Abstract

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The closure of leaf stomata in response to soil moisture deficits is a commonly observed phenomenon for which the mechanism is as yet unknown, hindering scientists who are interested in predicting the exchange of gases and energy between vegetated surfaces and the atmosphere. To work around this problem, predictive models have relied on empirical relations and theoretical formulations of optimal stomatal control with regard to water use efficiency. This research examines both empirical and theoretical aspects of the problem, with a focus on savanna ecosystems. Savannas hold special interest for water limitation questions, due to their characteristic seasonal drought and their mixture of woody and herbaceous vegetation, whose relative dominance is correlated with climate but as yet is not consistently explained with regard to the vegetation form and function. The question of water limitation in savannas is approached from the angle of two disciplines that

have both addressed the question of optimal water useage through analytical means but between which there is as yet little linkage: hydrologists, plant ecophysiolgists. A linkage is forged through the interdisciplinary nature of biometeorology, by examining leaf level processes (plant ecophysiolgists) at the canopy to landscape scale (hydrologists) through an analytical framework.

At a California blue oak savanna site, this research performs the first, full continuous partitioning for a savanna of evapotranspiration from the understory and tree layers through sap flow and eddy covariance measurements over seasonal cycles. Advanced statistics are used to identify the non-linearities in responses of canopy stomatal conductance, G_V , to meteorological drivers, and in particular the critical soil moisture points for blue oak water stress are identified. Apparent coordination in the seasonal use of water and energy resources in the out-of-phase phenology of the grasses and trees hints at optimization between growth forms for the annual useage of water in this Mediterrean ecosystem.

Applying the probabilistic ecohydrological optimality model of hydrologists Rodriguez-Iturbe and co-workers (2001), the different levels of statistical water stress experienced by the grasses and trees are differentiated during the different seasons helps explain their out-of-phase growth periods. The model is an analytical, equilibrium soil moisture balance model, which incorporates the decline in plant transpiration with soil moisture deficit, and yields interesting insights in constraining the plant root depth parameterizations to fit observed soil moisture probability density functions, hinting at the possibility of hydraulic lift.

However, this hydrologists' model's lack of inclusion of the role of energy, the driver

of transpiration, motivates an examination of the question of optimality as developed by plant ecophysiolgists in leaf gas exchange models. It is found that their complementary lack of inclusion of a soil moisture budget in turn limits their leaf level optimality models, since there is no clearly specified constraint for the optimality criterion. Thus, this research proposes a complete optimality model that clarifies the necessity of linking both leaf and landscape scales, the work of both ecophysiolgists and hydrologists. A new mathematical framework is required, that of stochastic optimal control, in which the plant's stomatal conductance is steered by expectations of future water availability at the landscape scale, which have been made by natural selection. Thus, this framework incorporates adaptation to climate as well as response to immediate environmental conditions. The roles of long-term (genetic), seasonal, and short-term (hourly) variation are explicitly distinguished, with the inputs to the model being solely climate and genetically constrained vegetation characteristics (leaf size, rooting depth), and outputs being the seasonal courses of photosynthetic capacity (V_{Cmax}) and leaf area index (LAI) and the time course of stomatal conductance.

This research adds to the database one of the more complete budgets of ecosystem fluxes of water vapor, increases coverage of arid and savanna ecosystems in the flux measurement community, and clarifies the meaning of optimality of water useage at leaf and landscape scales.

Dr. Dennis D. Baldocchi
Dissertation Committee Chair

This thesis is dedicated to:

Attilio

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Chapter 1

Introduction: Stomatal conductance and drought

If, therefore, λ has biological significance, it is that of a plant physiological parameter fashioned by evolution in the context of an environment having certain statistical properties. -I.R. Cowan, 1977

1.1 Overview

The λ to which I.R. Cowan refers in the above quote is the "cost of water" with respect to assimilation of carbon, in his founding attempt to model leaf conductance of water vapor and carbon dioxide using an optimality framework. The meaning of this λ has motivated, inspired, and puzzled researchers in subsequent attempts to further develop the optimality theory of leaf gas exchange, as all must eventually acknowledge the truth and elusiveness of Cowan's above statement in defining: what is "optimal." This research seeks to clarify the variety of angles with which the problem of modeling leaf stomatal

conductance has been approached. In doing so, a theoretically sound model of leaf stomatal conductance will be laid out for the plant ecophysiology, hydrology, and atmospheric science communities, in particular with the desire to account for conditions of drought, in the spirit of Cowan's above observation. It will be found that an optimality model of leaf gas exchange must ultimately be constrained at the landscape scale, emphasizing the necessity of linking the small and large, short and long scales in biophysical models that seek to address biogeographic questions. The lack of such a model is currently a major stumbling block in predicting ecosystem-level carbon and water balances and the general circulation patterns of the atmosphere. Particularly with respect to the impacts of global change on the distribution of the world's terrestrial vegetation, it is critical that scientists understand how plant stomatal control is a function of the probabilistic environment.

Plants both respond to and exert controls on climate, from their functioning at the leaf level, to their cumulative effects as cover over the landscape, to their long-term adaptations to climate through growth form and phenology. Many of the variations in plant form and function are adaptations to the constraints of the local climate regime, and at the same time the climate regime is a function of the plant influence on the energy balance and exchange of gases. To understand this interaction, a long-time focus of research has been on leaf gas exchange in the processes of photosynthesis and transpiration. Plants control gas exchange through leaf stomata, which adjust in aperture in response to meteorological drivers and plant physiological status. Under un-stressed conditions, stomatal conductance is well predicted by scientists' current knowledge of the biochemistry of photosynthesis and the physics of gas diffusion through the stomata. It is the stomatal adjustment under con-

ditions of soil moisture deficit that still is not well understood and which can lead to large errors in predicting fluxes. It is this phenomenon that is focused on here through three different approaches: through measurement of conductances and responses to meteorological drivers in a semi-arid ecosystem; examination of the vegetation functional types' experience of water stress in the context of the ecohydrological equilibrium model of Rodriguez-Iturbe, et.al. (2002); and proposal of a new model of stomatal conductance based on stochastic optimal control, which, given the phenomenon of seasonal drought, links leaf and landscape spatial scales, and short-term (meteorological conditions) and long-term (adaptation to climate) time scales. The ecosystem type of particular interest is a savanna system, whose characteristic seasonal drought and heterogeneous mixture of scattered woody vegetation over an herbaceous layer have held special interest for ecophysiologists, hydrologists, and climatologists examining the role of water limitation in structuring ecosystems. The guiding hypothesis is that optimality of leaf gas exchange is a function of and cannot be independent of landscape optimality of water usage, which may be characterized by the statistical climate environment.

This introduction provides background on the pitfalls in identifying drivers of stomatal control in field measurements, discusses the consequent challenges in modeling stomatal control under drought, and outlines the chapters to lead toward the kind of optimality framework that is required for this problem. In the course of these discussions and developments, this research must necessarily bridge the soil-vegetation gap – that is, the hydrology-plant ecophysiology gap – in the prediction of evapotranspiration (and therefore also carbon assimilation) under drought through optimality modeling. The critical point

of intersection between the two fields occurs in that regime where plants experience soil moisture deficits and therefore actively control the transfer of soil water to the atmosphere through their control of leaf stomatal conductance: not only energy but also biology constrain evapotranspiration. Optimality modeling is a top-down approach that allows one to bypass the bottom-up treatment of the details of plant anatomy and biochemical adjustments that are poorly known or difficult to quantify. The view is that plant stomatal behavior ultimately subsumes the suite of details as functioning together for overall adaptation to the soil-climate regime. Stomata behave to use the available energy and water “optimally” for survival and productivity at the individual and landscape scales. The precise definition of this “optimum” will be developed fully in the course of this thesis. In the process, not only leaf level controls will be identified, but also plant morphological and phenological characteristics that are a function of the soil-climate regime and that must inevitably be coordinated with stomatal behavior.

1.2 Plant physiology under drought: why it’s messy to model the soil moisture–stomatal closure connection

1.2.1 Drought tolerance mechanisms

In terms of overall plant strategies for survival in water-limited situations, there are numerous mechanisms that determine the water usage of the plant, both in response to immediate environmental variations and as strategies over the course of a growing season and longer. Jones (1992) provides one way of categorizing these mechanisms in Table 1.1.

Drought survival mechanisms (from Jones, 1992, Chapter 10)	
1. Avoidance of plant water deficits	
(a) Drought escape - short growth cycle, dormant period	
(b) Water conservation - small leaves, limited leaf area, stomatal closure, high cuticular resistance, limited radiation absorption	
(c) Effective water uptake - extensive, deep or dense root systems	
2. Tolerance of plant water deficits	
(a) Turgor maintenance - osmotic adaptation, low elastic modulus	
(b) Protective solutes, desiccation tolerant enzymes, etc.	
3. Efficiency mechanisms	
(a) Efficient use of available water.	
(b) Maximal harvest index (e.g. a mean or maximum annual productivity goal)	

Table 1.1: Drought survival mechanisms and strategies. (Jones, 1992).

Thus, plant utilization of water and maintenance of adequate leaf water potentials for metabolic health can be a function of phenology, morphology, anatomy and physiology, and biochemistry.

1.2.2 Modeling physiological influences on stomatal closure

Viewing the above mechanisms, we must ask: how many of these mechanisms and strategies must a stomatal conductance model of drought take into account, in order to avoid empirical oversimplification? Can most of these features of drought tolerance emerge from a more unifying theory about plant water usage?

Let us review what makes particularly prediction of stomatal response to drought so difficult in modeling investigations. In general, in terms of plant water status, it is known that stomatal closure during drought is correlated with critical levels of leaf water potential and the presence of the hormone abscisic acid (ABA) (Jones, 1992; Tardieu, 1993; excellent review by Sauter, et.al., 2001). Note that environmental conditions also influence stomatal

conductance. The influence of physical drivers are fairly well understood and will be reviewed later, but the role of plant physiological status is what is imprecisely understood, so this aspect is focused on here.

Leaf water potential

Leaf water potential (the sum of hydrostatic, osmotic, matric, and gravitation components) affects cell turgor and biochemical processes. Stomatal conductance is most closely associated with the hydrostatic pressure component. Reduced pressure in the guard cells of stomates will cause them to close down, reducing diffusion of water out of the leaf, and allowing the partial pressure to build back up again. Such a cycle of opening and closing is the normal behavior in a non-stressed plant as the stomata regulate gas exchange (Nobel, 1999). Under drought conditions, stomatal closure is induced through three possible explanations: 1) stomata close to control against cavitation damage under very low leaf water potentials (Cochard, et.al., 2002), 2), the hormone ABA signals the presence of soil moisture deficits (Gollan, et.al., 1986; Tardieu, et.al., 1996; Liang, et.al., 1999), and 3) low leaf water potential may reduce photosynthetic capacity, since water is part of the dark reaction regeneration of NADP (Nobel, 1999), and low cell turgor can limit cell expansion (Jones, 1992). Currently, there are as yet no mechanistic explanations for any of the correlation of these phenomena with stomatal closure. Recovery of stomatal conductance has been observed to lag recovery of leaf water potential following soil re-watering, possibly due to the lag in the recovery of photosynthetic capacity if reduced by drought stress, but there is no mechanistic explanation yet why (Liang, et.al., 1999). Photosynthetic capacity determines how quickly carbon dioxide can be fixed, and hence directly affects the gradi-

ent for diffusion of CO₂ into the leaf. Extensive data show that stomata also regulate the ratio of the internal CO₂ concentration to the ambient concentration in order to maintain a diffusive gradient; therefore, reduced photosynthetic capacity will reduce the rate of CO₂ uptake and reduce stomatal conductance.

How can one predict the primary plant physiological indicators of drought, leaf water potential and ABA? The difficulties can be categorized as those having to do with 1) representation of the static hydraulic architecture of the plant as it affects leaf water potential, 2) prediction of phenological variation in that architecture (with respect to growth and senescence of roots and leaves), and 3) understanding of biochemical mechanisms that protect the plant against drought. The details of these issues are described below.

Hydraulic conductivity

The pathway for transpiration from the soil through the plant and to the atmosphere is a function of the plant anatomy and architecture that change along the roots, stems, and leaves, and which may also change seasonally. Thorough reviews of plant conductive anatomy may be found in textbooks, such as that by Nobel (1999), and the nature of flow through porous media is described in engineering textbooks. A review of research issues about hydraulic architecture is provided by Meinzer, et.al. (2001), with regard to knowledge of the quantitative ratios between components of the pathway of transport, the mechanisms for flow, and the adaptation of hydraulic architecture to environment. According to theoretical work by Enquist, et.al. (1998), it appears that the maximal ability of trees to transport water through the xylem is directly proportional to a roughly 3/4 power of the tree mass, across all species, a result that matches closely to empirical evidence.

This elegant and simple relation provides insight into the energetic limitations on plant productivity, but, of course, does not address the temporal (diurnal, seasonal) variations that plants undergo, or the variation in functional types within an ecosystem, and there is still unexplained scatter around this $3/4$ power law. Therefore, research continues on the representation of hydraulic conductivity in plants in order better to understand the soil-vegetation-atmosphere pathway.

The conventionally accepted mechanism of water movement through the plant is capillary flow, because the plant vessels and pores can be viewed as bundles of tubes or as a porous conductive medium (Tyree, 1997). The theory is known as the “cohesion-tension theory” of sap flow, as introduced by Henry Dixon and Charles Joly at the end of the 19th century (Nobel, 1999). This theory views the plant as a rigid medium that supports extremely negative water pressure potentials at the leaves in order to afford continuous flow along a gradient of potentials. Flow can be broken due to cavitation or embolism, which may be either permanently damaging, or may be alleviated through leakage into the conductive vessels from surrounding parenchyma. This theory has been challenged by the controversial “compensating pressure theory” (Canny, 1995, 1998), which asserts that the expansion and contraction of plant tissue with changing tissue water contents acts as a pumping mechanism to maintain flow. Thus far, the latter theory is still untested and therefore modeling investigations cannot use it (although one may find similar frameworks in the civil engineering literature on pumping of fluids from soils; Tadeusz Patzek, personal communication). Therefore, modeling investigations based on the cohesion-tension theory are reviewed below, as these give insight to the complications that arise in trying to ac-

count for the many details in the plant hydraulic pathway. In particular the problems of representing hydraulic conductivity for trees and tree canopies will be discussed.

The simplest and most common way to represent bulk flow through any medium is as diffusion, i.e. as flow between different potentials, through a medium with a given resistance (or conductance). Therefore, it is natural to make a first attempt to represent the hydraulic conductivity of a woody plant this way, parameterizing the roots, stem, and branches with bulk resistances, as diagrammed in Figure 1.1. There are also capacitance effects, because the water potential and resistances along this pathway are affected by the saturation level of the tissue, since the elastic modulus of the tissue directly relates the volume of the tissue and wood water content or water potential (Perämäki, et.al., 2001). The most significant effect results in diurnal and seasonal fluctuations in tree bole diameter, this capacitance indicated by c_{stem} in Figure 1.1 (Holbrook, 1995).

A basic modeling example which does not include capacitance effects is the model of Williams, et.al. (1996), which represents a tree canopy and root system as a homogeneous, layered system of resistances in series, numerically simulating the gradient in water potential from soil to leaf. The parameterization of this model relies on an exhaustive dataset by Tyree, et.al. (1993b), in which a whole tree was cut up to measure the hydraulic conductivity of its individual stem segments, with the bulk conductivities then calculated through use of a branching model. Such empiricism provides reference data, but is impractical to use for diverse biomes and requires unclear simplifying assumptions for application at the ecosystem scale. Water storage effects (capacitance) in the tree bole add more complications, as change in tissue saturation and bole shrinkage and swelling can fluctuate on a diurnal basis

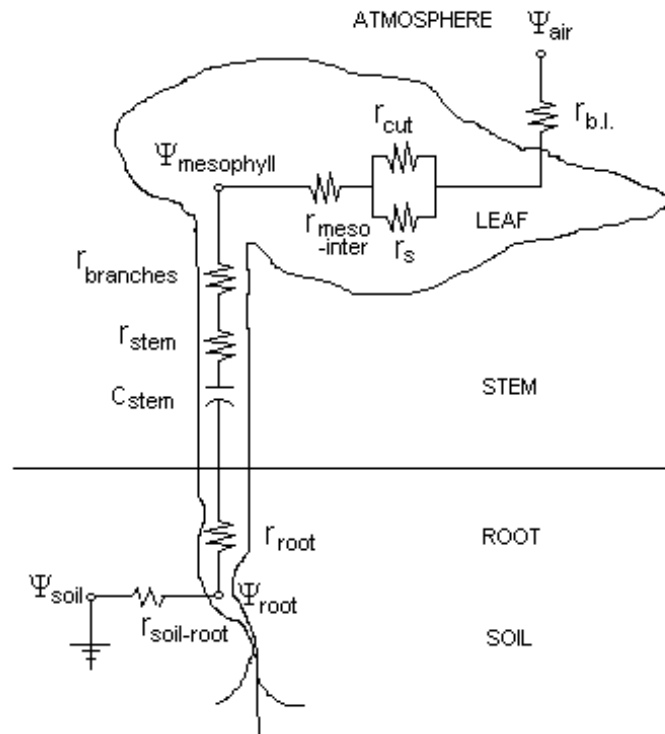


Figure 1.1: Circuit diagram of pathway of water potentials and resistances to sap flow and water vapor diffusion through a woody plant, with circuit ground (inverted triangular hatchmarks) ending in the soil. r_x - resistance, c_x - capacitance, Ψ_x - potential.

(tested model by Perämäki, et.al., 2001), due to night-time recharge (Goldstein, et.al., 1998) or exchange of bark moisture (Zweifel, et.al., 2001). The daily contribution of such capacitance effects has been observed to be 9-15% of total daily transpiration in tropical trees (Goldstein, et.al., 1998).

Pipe model theory provides a theoretical framework for the relation of sapwood area to leaf area, since the supply of sap by the stem must necessarily limit the evaporative area of the leaves. This framework yields generally tight statistical relations, but it is less useful for estimating hydraulic conductivity, as the distribution of conductive vessels is subject to such complicating factors as the tortuosity in vessel paths and variation in vessel size; the use of this theory must rely on measurements of particular species and therefore it is hard to extrapolate (Chiba, 1991, 1998; Mäkelä, 1986; Rennolls, 1994; Waring, et.al., 1982).

Früh and Kurth (1999) have done the most realistic modeling of tree hydraulic conductivity to date, formulating a numerical model that explicitly describes the tree as a porous medium (of homogeneous porosity), including separation of branches and loss of hydraulic conductivity with cavitation. The investigators also used Tyree, et.al.'s (1993b) data set to check the model performance, but more validation is required. The problem of anatomical heterogeneity within stem segments, the great detail required for this model, and its computationally intensive nature prevent its widespread application.

In addition to being a function of the tree architecture and level of saturation, tree hydraulic conductivity is also affected by solutes, which change the osmotic potential, and which may adjust in concentration in response to drought (Jones, 1992; Momen, et.al., 1994;

Thomas, et.al., 2000). This osmoregulation is one of the many physiological responses that have been observed in correlation with ABA, whose mysteries are further reviewed below. Thus, modeling tree hydraulic conductivity, even given known architecture, is still a highly empirical, elusive problem.

Temporal variation in hydraulic conductivity

Even given an extensive data set for hydraulic conductivity on a tree like that of Tyree, et.al. (1993b), the temporal variation of the root and stem systems further complicates attempts to parameterize resistance-type models. Root growth and senescence may be due to responsiveness to nutrient availability (Eissenstat, et.al., 1997), location and saturation of soil moisture (Thomas, et.al., 2000), and phenological timing (Eissenstat, et.al., 1997). Root acquisition of soil moisture can further be enhanced by the presence of fungal hyphae (Nobel, 1999) and the phenomenon of hydraulic lift (Caldwell, et.al., 1998). Therefore, the root system may not always immediately provide full access to the available soil moisture, or it may have greater access than a simple model might predict, and in general the root to shoot ratio in plants adjusts in response to needs for below-ground resources. In tree stems, hydraulic conductivity can change diurnally and seasonally due to storage and cavitation in the stems and seasonal changes in the diameter of new conductive vessels (in ring-porous trees) (Nobel, 1999; Hubbard, 2001). Seasonal change in leaf area index can alter the evaporative demand of the tree, thus altering conductance in the canopy.

1.2.3 Biochemical responses to drought

The biochemical response of a plant can also impact stomatal behavior. As mentioned earlier, osmotic adjustment to maintain turgor can maintain conductivity (Momen, et.al., 1994; Thomas, et.al., 2000). Meanwhile, the conductance through the leaves may be reduced during drought due to impacts on cell processes and reduction in photosynthetic capacity. Root production of the hormone abscisic acid (ABA) can signal stomatal closure in the leaves to prevent cavitation, thereby maintaining water potentials and cell turgor while limiting transpiration below the evaporative demand of the environment (Tardieu, 1993). Jones (1992) provides a catalog of observations of potential responses to ABA, the strongest correlations between water stress and ABA being short-term decreases in stomatal conductance and photosynthesis, and long-term inhibitions of growth, cell division, and cell expansion. Although these phenomena have all been observed, the mechanisms that induce them are still poorly understood and therefore not possible to model, yet. For example, the mechanism that induces root production of ABA is not known; the transport of ABA from root to leaf is not clear; and researchers have difficulty correlating leaf ABA content with stomatal closure, because sequestration of ABA occurs in certain cells, preventing sensing by the stomates; furthermore, the mechanism for release of this leaf ABA is not known (Mambelli, personal communication). Modeling of the influence of ABA has been done in an interesting conceptual manner by Tardieu, et.al. (1993a), in which the dilution of ABA stored in the tree bole through sap flow is correlated with stomatal closure, but this attempt is still highly empirical.

In summary, the plant's active access to soil moisture, changing water conductivity

through the plant, and changing biochemistry all affect the leaf status and hence stomatal behavior. The complexity and dearth of knowledge about the variety of physical and biochemical mechanisms limits scientists' abilities to include even the most significant of them in a mechanistic model of stomatal response to drought. Optimality modeling, therefore, offers an alternative, top-down approach to subsume these mechanisms within a framework based on theories of plant adaptation to climate.

1.3 Ecosystems with seasonal drought stress: savannas

Savanna ecosystems hold special interest for water limitation issues, because the seasonal drought that characterizes their climate regime is the accepted but as yet not fully explained controller of the savanna mix of scattered woody vegetation over an herbaceous layer (Scholes and Archer, 1997). Because water limitation in savannas is manifested in both the open canopy cover or leaf area of its woody vegetation (Woodward, 1987) as well as stomatal control during the drought season (Scholes and Walker, 1993; Prior, et.al., 1997), this ecosystem type is a natural model system with which to investigate optimality models of stomatal responses to drought, when the response is viewed as constrained by landscape-level resources.

The heterogeneous mixture of vegetation in savannas has been viewed, according to some theories, as stable due to niche partitioning between the woody and herbaceous functional types, or unstable with shifts following interannual climate variability or other disturbance. Given that the savanna share of the terrestrial surface has been estimated as high as 30% (Werner, et.al., 1990), it is important not only to be able to predict their

immediate exchanges of trace gases and energy with the atmosphere in general circulation models, but also to be able anticipate shifts in the woody/herbaceous mix, which could potentially alter the carbon exchange of the atmosphere at a magnitude on par with tropic rainforests (Chris Field, personal communication). The shifts in the carbon balance would be due not only to above-ground but also below-ground effects with changes in soil organic carbon and root biomass: among all vegetation sclerophyllous vegetation have the highest rooting depths (Schenk and Jackson, 2002) and root biomass density (second only to tropical evergreen forests; Jackson, et.al., 1996), but the relative contribution of grasslands versus woody vegetation to soil organic carbon can vary, depending on precipitation regime (Jackson, et.al., 2002). Therefore, understanding this fine balance for savannas is critical for predicting shifts in the global carbon balance.

The classic explanation of tree-grass coexistence by Walter (1971) is that the herbaceous vegetation and trees have different rooting depth niches, with grasses intercepting shallow soil moisture first after a rain, and the trees penetrating to deeper soil moisture. Peter Eagleson (Eagleson, 1982; Eagleson and Tellers, 1982; Eagleson and Segarra, 1985), a hydrologist, drew upon this idea in formulating an ecohydrological theory to determine the equilibrium mixture of herbaceous versus woody cover in a water-limited climate. The idea of root niche partitioning has since been shown not to be completely general for all savannas (e.g. same rooting depths for all species in Nylsvley, South Africa; Scholes and Walker, 1993), motivating other theories about water use strategies and coexistence, such as a horizontal minimization of landscape water stress (Rodriguez-Iturbe, et.al., 1999a). Prediction of savanna vegetation structure, thus, remains an open research question. Nu-

merous other ecological factors are involved, also, but climate is still the broadest scale, primary controller that has yet to be satisfactorily explained.

In this thesis, therefore, one savanna system is investigated through detailed measurements of transpiration and plant physiology, to provide insights and provoke hypotheses through observations about the different vegetation functional types and their seasonal behaviors.

1.4 Chapter organization

The presentation here is structured to move gradually from the empirical and particular to the theoretical and general. In Part I, detailed measurements of vegetation water use in a savanna ecosystem create a concrete set of expectations of some type of optimal control – within and between functional types – in this system. In Part II, the theory is reviewed and developed to allow linkage of the full suite of spatial and temporal scales necessary in specification of the optimality criterion.

In Part I, Chapter 2, are presented the detailed measurements of transpiration and plant physiological status in a California blue oak savanna. These data offer the first such detailed, continuous partitioning of the fluxes of the overstory and understory layers in a savanna ecosystem. This partitioning of the tree and understory contributions to evapotranspiration over seasonal cycles allows assessment of how the functional types trade off in the usage of water and energy resources from the wet winter through the summer drought in this Mediterranean climate. For the tree layer in particular, the response functions of canopy stomatal conductance to meteorological drivers are derived, with special interest in

identifying soil moisture critical points in the behavior of the trees. The seasonal courses of the two primary vegetation functional types in this ecosystem lead then to speculation about the climate adaptations of their growth forms and the optimality of their use of water through seasonal change. Forthcoming detailed measurements on soil and bole respiration in this system will eventually allow carbon assimilation and the water use efficiency of the system to be addressed, and future modeling with the model MEDRUSH (Osborne, et.al., 2000) will provide potential photosynthetic parameters to compare to actual values.

In Part I, Chapter 3, the differences in water stress experienced by the grass and tree layers in the California blue oak savanna ecosystem are examined, in the context of a probabilistic ecohydrological equilibrium model of Rodriguez-Iturbe and co-workers (Rodriguez-Iturbe, et.al., 1999b; Rodriguez-Iturbe, et.al., 2001; Porporato, et.al, 2001; Laio, et.al., 2001a; Laio, et. al., 2001b). This analytical equilibrium model is a hydrologist's attempt to incorporate the role of water stress into the representation of vegetation transpiration. It provides descriptive measures of the probabilistic soil moisture regime by season for each vegetation functional type, given their morphological features *a priori*, and thus provides a means to explain the coexistence of these types. With its focus on the soil moisture balance and precipitation patterns, this work by hydrologists yields insight into the importance of soil properties and plant rooting depth. However, although it is a predictive model with respect to soil moisture, it is only descriptive with respect to vegetation and leaves out such important climatic factors as energy availability, and plant constraints such as the biochemistry of photosynthesis. Acknowledging these simplifications with regard to ecosystem productivity, the hydrologists pave the way for Part II.

In Part II, Chapter 4, the history of vegetation-climate optimality investigations are reviewed, from early correlation mapping schemes of biogeographers and simulation models of climatologists, to ecohydrological equilibrium models of hydrologists, and finally to models of leaf gas exchange by plant ecophysiologicalists. The basic problem is discussed of defining what is "optimal", offering refinements to the models of leaf gas exchange, but ultimately proposing that a new framework is required: optimality of stomatal control cannot be defined at the leaf scale alone, but must account for resource constraints, which occur at the landscape scale. Furthermore, stomatal behavior with respect to climate is responsive to both immediate meteorological drivers as well being a function of longer-term plant adaptations to climate. The new framework that can accommodate these requirements is given in the next chapter.

In Part II, Chapter 5, a model of stomatal conductance is formulated within the framework of stochastic optimal control. The model includes scientists' current knowledge about photosynthesis and leaf gas exchange, incorporates hydrologists' probabilistic representation of climate, and seeks to subsume the messiness of plant anatomy and biochemical responses to drought under an optimality criterion with regard to water useage. The optimality criterion is based on the vegetation's expectations of future available water, given current conditions. The model takes as inputs only climate and soil parameters, and yields families of simultaneous solutions for these critical vegetation characteristics: the temporal course of leaf stomatal resistance, leaf area index, photosynthetic capacity. It is expected that there is no one ideal configuration of vegetation types for a given climate, and that different vegetation may have different optimality strategies; therefore, the vegetation

parameters of rooting depth and leaf size may be specified exogenously, yielding different patterns for a variety of optimal water use strategies. Simulations on climate data and climate scenarios are the scope of future work.

Part I

Partitioning overstory and understory fluxes of water vapor in a spatially heterogeneous ecosystem subject to drought

The guiding null hypothesis, as discussed previously, is that vegetation (and soil) in a natural ecosystem has evolved to make full use of the water and energy resources within that climate regime, such that transpiration of water by the vegetation is the maximum possible, given the constraints of available water and energy in time. That is, in a system at equilibrium with climate, no water is lost for lack of vegetation to use it. How can a real system be measured to test this hypothesis?

Savanna ecosystems offer the ultimate challenge to ecologists, hydrologists, and biometeorologists due to their heterogeneity in vegetation structure (in form, function, and spatial distribution) and the seasonal drought that has been a hypothesized driver of that heterogeneity. In particular, savannas are characterized by the coexistence of an open canopy of trees over an herbaceous understory. The dynamics of many savannas are in addition heavily driven by the influence of fire and herbivory, but the biome-scale limit on the global distribution of savannas is ultimately climate. Here, the main focus is on the influence of water and energy resources and their utilization by the two savanna vegetation layers, with two main guiding questions: 1) Are the tree and herbaceous layers coordinated in their seasonal growth cycles to obtain an "optimum" utilization of water and energy resources? 2) How can the two vegetation components be measured best to partition their contributions to the ecosystems exchange of water vapor, carbon dioxide, and energy with the atmosphere?

The motivations for measuring the seasonal variation in water usage and carbon uptake of a savanna ecosystem and its components are threefold: 1) global change science needs better understanding of how to quantify and predict biosphere-atmosphere fluxes in

spatially heterogeneous ecosystems using satellite data, and 2) the mechanisms of drought response of vegetation are poorly known, for which the seasonal drought that defines savanna vegetation dynamics provides a model ecosystem; 3) the biome-scale determinants of the compositional balance between woody and herbaceous vegetation in savannas are still poorly quantified.

Measurements of ecosystem fluxes are complicated by spatial sampling, scaling, and coupling issues, and by the necessity to match measurements to the processes of interest for predictive models (Ruimy, et.al., 1996). Ground sampling becomes more laborious as the need for greater attention to spatial variation increases (separating soil and microbial versus vegetation components, vegetation components from each other, and accounting for small-scale environmental variability). Extrapolation from smaller to larger scales (leaf to plant, leaf to landscape, plant to landscape) must balance the need for simplicity versus accuracy, and must identify the non-linear relations between scales. And estimating vegetation exchange with the atmosphere becomes less straightforward with tall and open canopy systems, as the similarity between mass, heat, and momentum exchange becomes decoupled (Jarvis and McNaughton, 1986). Prediction of fluxes through modeling is made difficult by these scaling and coupling issues, and by scientists' current lack of knowledge of the mechanisms for vegetation stomatal control under drought. Finally, temporal quantification of the physiological behavior of savanna vegetation over seasonal cycles is sorely needed in order to predict potential vegetation shifts with climate change, as the balance between woody and herbaceous vegetation can have a critical impact on the regional water budget, surface energy balance, global carbon budget.

Up till now, a variety of measurement techniques have been developed for measuring soil and vegetation fluxes of water and carbon dioxide and responses to meteorological drivers, but they have seldom been used simultaneously to perform a full partitioning of the various critical ecosystem components or long term to fully capture seasonal vegetation dynamics. Leaf level (chambers, e.g porometer, branch bag), individual plant and plot level (xylem sap flow, lysimeter balance, biomass harvesting), and integrative (eddy covariance, aircraft) vegetation flux measurement methods (and stable isotopes and leaf water potential, which span these scales) are now common, but they have seldom been used simultaneously or long term to perform a full identification of physiological response functions and full ecosystem partitioning for natural forested systems. Of these techniques, only sap flow and eddy covariance techniques offer the ability to continuously monitor fluxes and without physical disruption to the environmental conditions of the object of study. Because the eddy covariance technique measures net surface fluxes, it is able to monitor net ecosystem exchange (NEE) of trace gases and energy, that is, the net sum of instantaneous inputs and outputs between the land surface and the atmosphere, at the scale of a kilometers, depending on tower height and wind speed. The practice of measuring NEE with eddy covariance towers above an ecosystem has now become widespread, such that multi-year datasets are increasingly available in diverse ecosystems (Baldocchi, et.al., 2001). Researchers additionally perform other ground-level measurements to identify the contributions of different ecosystem components to NEE, but there have been few attempts to measure all components directly. In forests, separating out the contributions of understory vegetation and the soil has been difficult due to the sampling issues mentioned above. Also, the eddy

covariance method is less reliable below tree canopies where the wind regime is still or disrupted by local bluff bodies, such that the velocity, time, and length scales of turbulence are not homogeneous as in the surface boundary layer above the canopy (Raupach, et.al., 1996; Baldocchi, 1997b).

The most complete efforts to date in terms of partitioning fluxes are the BOREAS experiment (Hogg, et.al., 1997; Saugier, et.al., 1997; duration one growing season), the HAPEX-Sahel campaign (Goutourbe, et.al., 1997; duration 2 months), the Hartheim synthesis campaign (Bernhofer, et.al., 1996b; duration one month), a study of a *Pinus radiata* plantation in New Zealand (Whitehead, et.al., 1994; 2-3 day campaigns spread over a year), and a short campaign in New Zealand (Köstner, et.al., 1992; Kelliher, et.al., 1992; two 3-day campaigns in one season). Savanna ecosystems have been the last terrestrial ecosystems to be measured for fluxes (HAPEX-Sahel, Goutourbe, et.al., 1997; Brazilian cerrado, Miranda, et.al., 1997; Australian eucalypt savanna, Eamus, et.al. 2001), and these few efforts attempted vertical partitioning only indirectly by estimating woody vegetation water use through the difference between eddy covariance measurements and extrapolations of soil chamber measurements (Eamus, et.al., 2001). All of these efforts have been short-term campaigns in different seasons, but not continuous.

Here for the first time is presented a year-long partitioning of the understory, overstory, and tree-covered vs. open areas of the water vapor, carbon dioxide, and energy fluxes of a savanna ecosystem, using above- and below-canopy eddy covariance, sap flow measurements, and time series of leaf sampling. This is also the first such full long-term partitioning for a Mediterranean ecosystem. The site is a California blue oak (*Quercus*

douglasii)/annual grass-dominated savanna in Ione, California, which was chosen for its well-defined vegetation structure: one dominant tree species randomly distributed, no shrub layer, and an annual grass layer whose growing season is out of phase with that of the trees, which are deciduous, with only about 1.5 months overlap, such that the fluxes of the two layers, as well as the open and canopy-covered areas, can be distinguished with certainty. Thanks to the open nature of the understory, the wind regime below the tree canopy is still suitable for eddy covariance measurements.

The next chapters present results from performing such a partitioning in a California blue oak and California annual grass savanna. The results of sap flow measurements are detailed, with respect to technique for the ring-porous architecture of blue oaks, scaling up from tree measurements to the stand scale, comparison to eddy covariance measurements, and analyzing these estimates of tree water use with respect to tree physiological characteristics and response functions to meteorological drivers. Interpretations of the flux partitions are then discussed with respect to optimal water usage in this ecosystem, in terms adapted usage of water and energy resources to maximize gross and net carbon uptake at the leaf and landscape scales. Finally, speculations are made about how a savanna ecosystem like this may shift its gross carbon uptake in response to climate change, due to leaf-level responses as well as vegetation cover change.

Chapter 2

Daily and seasonal patterns of transpiration and xylem water potential in a California blue oak savanna and the response to drought

Abstract: This research offers the first complete data set for the annual water usage of a California blue oak canopy in relation to meteorological driving variables. Data include one year of sap flow measurements scaled up to the stand level in a California blue oak (*Quercus douglasii*) savanna, and above- and below-tree canopy eddy flux measurements, covering both diurnal and full seasonal variation from wet winter through dry

summer. Leaf area index and leaf water potential were also recorded on a bi-weekly basis from the peak growing season through the summer dry-down. Accompanying data for the study site in Ione, California, include seasonal courses of leaf gas exchange, and productivity estimates from litterfall. Tree canopy conductance is calculated from inversion of the Penman-Monteith equation after separating out the understory fluxes, and the responses of canopy conductance to driving variables, including soil moisture, are derived through advanced statistical analysis. Critical soil moisture points are uncovered for oaks at relative extractable water contents (REW) of 0.34 for the onset of water stress, and 0.28 for the onset of wilting. Stand-level transpiration as measured by sap flow techniques is compared to eddy covariance measurements. It is found that sap flow measurements fail to capture the spring peak tree transpiration, due to disruption of the outer, larger vessels in the ring-porous anatomy of the oaks. Eddy covariance measurements show peak tree transpiration of 2.2 cm d^{-1} , while sap flow only shows 1.4 cm d^{-1} . However, during the summer, both measurement techniques converge to the same values, when the smaller tree vessels are responsible for maintaining sap transport; this indicates that the eddy covariance technique of differencing above- and below-tree fluxes is adequate for partitioning tree from understory fluxes. The blue oaks exhibit a remarkably steady linear decline in transpiration rates during the summer, in sharp contrast to the exponential decline of the pines following soil moisture trends, indicating the operation of drought tolerance mechanisms in the oaks. The seasonal patterns of actual evapotranspiration (AET) and potential evapotranspiration (PET) for the annual grass versus tree layers hint at coordination among functional types in the utilization of water and energy resources over seasonal changes, switching from energy-

limited transpiration by the drought-avoiding grasses in the wet winter to water-limited transpiration by the drought-tolerant oaks in the dry summer.

2.1 Introduction

Savanna ecosystems are defined as consisting of an open canopy of scattered trees over an herbaceous understory, a vegetation structure that arises in warm climates with seasonal water deficits (Walter, 1971; Scholes and Archer, 1997). This ecosystem type occurs throughout Africa, Australia, and South America, as well as Mediterranean climates, and is known also as *dehesa* in Spain, *cerrado* and *caatinga* in Brazil, *miombo* in Angola, and *llanos* in Venezuela and Colombia. Estimates of the savanna share of the terrestrial surface range as high as 30% (Werner, et. al., 1990). In Defries and Townsend’s global data set (1994), the category of “wooded grassland” accounts for 17%, the single largest land cover type. The spatial and structural heterogeneity of savannas challenges scientists who seek to explain the balance between the two plant growth forms, whether ecologists focusing on community dynamics, hydrologists focusing on the water balance, or biogeochemists budgeting the fluxes of carbon and water. As shifts in the woody/herbaceous balance in savannas could potentially alter the carbon exchange of the atmosphere at a magnitude on par with tropical rainforests (Chris Field, personal communication), it is critical that scientists quantify the atmospheric exchanges of these two vegetation components, their responses to changing climate drivers, and what determines their relative dominance over the landscape.

This research provides the first full, continuous quantification of the diurnal and

seasonal water usage of the tree and understory components of a savanna ecosystem. These measurements are part of a larger effort to thoroughly quantify the fluxes of carbon dioxide, water vapor, and energy of the ecosystem and its components through biometeorological methods (Baldocchi, et.al., in preparation; FLUXNET, <http://www.eosdis.ornl.gov/FLUXNET>, Ione, California, savanna site). Because seasonal water deficit is the dominant controller of the tree-grass balance in savannas, and because classical theory (and controversies) about tree-grass coexistence in savannas centers on differential soil moisture access due to rooting depth (Walter, 1971), it is important to quantify first the magnitude and timing of water usage by the two vegetation types.

The field is expanded here by performing the first such full vertical and horizontal partitioning of fluxes in a savanna to distinguish the contributions of the tree and grass layers, and open grass areas versus areas under tree canopy, using eddy covariance and sap flow measurements. Furthermore, a first continuous data set is provided of the seasonal dry-down of a savanna. Previous efforts to quantify fluxes of savannas have been short campaigns (HAPEX-Sahel, Goutourbe, et.al., 1997; Brazilian cerrado, Miranda, et.al., 1997; Australian Eucalyptus savanna, Eamus, et.al., 2001) and have not continuously quantified the understory fluxes, and only one study has distinguished open versus below-tree canopy components (Tuzet, et.al., 1997). Water balance estimates of some savannas (tropical savanna, Nylsvley, South Africa, Scholes and Walker, 1993; Spain dehesa, Joffre and Rambal, 1993) have only been done through indirect difference techniques. For all ecosystem types, there have been few efforts to date to perform a full partitioning of forest understory and overstory fluxes, the most thorough attempts being those in the BOREAS campaign (Bal-

docchi and Vogel, 1996; Baldocchi, et.al., 1997; Blanken, et.al., 2001), in New Zealand Nothofagus forest (Köstner, et.al., 1992; Kelliher, et.al., 1992), in Oregon Ponderosa pine forest (Law, et.al., 1999), and North American temperate deciduous forest (Wilson, 2001). The latter study is the only one that was not a short campaign and which used the full suite of above- and below-canopy eddy covariance and sap flow measurements, as well as catchment and soil water budgets for a full year or longer.

The savanna ecosystem of this study is a California blue oak (*Quercus douglasii* H.&A.) and annual grass savanna, which occurs in a Mediterranean climate. California blue oaks are the most widespread of the California oaks, covering nearly half of the 3.0 million ha of California's hardwood rangelands (Standiford, 1997), ringing the Central Valley between 100 and 1200 m elevation (Barbour and Minnich, 2000) plus occurring in some minor coastal areas. Blue oaks occupy the most xeric limits of the oaks, and are especially noted for their drought tolerance (Muick and Bartolome, 1987), exhibiting drought deciduousness, phenotypic plasticity (Callaway and Mahall, 1996; Rice, et.al., 1993), hydraulic lift (Ishikawa and Bledsoe, 2000), and alteration of their osmotic potential to maintain cell turgor during soil moisture deficits (Momen, et.al., 1994), such that, among the oaks, they are able to maintain the most negative leaf water potentials (as low as -45 bar in saplings and mature trees; Griffin, 1973). They comprise the dominant tree species (range of 10-60% canopy closure) in open savanna environments with a continuous annual grass layer. Coexisting tree species in small numbers are grey pine (*Pinus sabiniana*) along the Central Valley and other oaks in the more mesic ranges of the blue oaks. Shrubs represent a fairly insignificant percent (<5%) of total woody cover (see Barbour and Minnich, 2000, for de-

tails). Research concerns about blue oak have centered on the tree impacts on understory productivity, and on concern about a lack of regeneration due to numerous potential causes (Muick and Bartolome, 1987; Swiecki, et.al., 1993).

To date, there is uncertainty as to what environmental factors limit the distribution of blue oaks – an uncertainty typical for savannas in general. The demographic structure of blue oak populations is "typically non-climax" (Barbour and Minnich, 2000), with uneven age structures indicating episodic regeneration. European settlement since the 19th century has introduced such changes as increased frequency of fire, replacement of native perennial grasses with annuals, and grazing by cattle, making it difficult to distinguish any particular factor in combination with climate as the determinant of blue oak growth and regeneration, or lack of it (Mensing, 1992).

Ecological studies of factors affecting natural blue oak regeneration include those examining impacts of grazing and herbivory (Bartolome, et.al., 1994; Bartolome, 1997; Borchert, et.al., 1989; Muick and Bartolome, 1987; Swiecki, 1993; Welker, 1990), fire (McClaran and Bartolome, 1989a), protective cover (Callaway, 1992; Swiecki, et.al., 1993). Population and community dynamics that may influence regeneration include masting behavior to increase seed set and avoid predation (but not in response to resource variation) (Koenig, et.al., 1994), and competition between grasses and blue oak seedlings for soil moisture and/or nutrients in laboratory experiments (Gordon, et.al., 1989; Gordon and Rice, 1993; Koukoura and Menke, 1995; Welker, et.al., 1991). Physiological studies have been conducted on blue oak seedling response to soil moisture availability (Momen, et.al., 1994; Muick and Baltolome, 1987; Kloss, 2000; and see studies of competition with grasses), with

some unpublished field experiments that show better survival of seedlings with additional water (Peter Hujik, The Nature Conservancy, personal communication).

From these studies, there is some consensus that additional soil moisture and protection against grazing by shrubs or rocky outcrops promote survival of blue oak seedlings. However, in the lab study by Kloss (200), in which seedlings were given dry, normal, and wet moisture treatments, seedlings with the middle treatment were the first to senesce their leaves. No conclusive explanation was given – possibly, seedlings in "normal" years senesce upon acquiring adequate storage for the following year, while seedlings in drier years must extend their growth longer to do so, and seedlings in wet years are adapted to expect a year without water stress and hence no need to senesce; but these are all conjectures. There is a suspicion that annual grasses adversely affect blue oak seedling survival indirectly by increasing herbivory by rodents in productive years (Bartolome, personal communication). Swiecki, et.al. (1993) believe that mature trees simultaneously promote seedling survival by moderating water stress, while also suppressing height growth due to shading, such that seedlings only increase growth upon death of the mature tree; this would imply that blue oak systems are at a carrying capacity with respect to tree density. Meanwhile, a oak tree removal study in the Sierra foothills showed that the 14% cleared land area was not large enough for the trees to have a significant impact on the overall hydrology of the area (Lewis, et.al., 2000). Overall, these ecological and watering studies are inconclusive about explaining blue oak stand structure with respect to disturbance, community dynamics, and soil moisture.

Biogeochemical cycling and productivity studies provide data on the influence of

the blue oak canopy on soil nutrient content (Callaway and Nadkarni, 1991; Dahlgren, et.al., 1997; Jackson, et.al., 1990) and on understory productivity (Bartolome, et. al., 1994; Callaway, et.al., 1991; Dahlgren, et.al., 1997; Jackson, 1990 ; McClaran and Bartolome, 1989b). Although soils directly under blue oak trees are clearly higher in nutrient content and soil organic matter than that in open areas, the balance between enhanced soil status versus overstory impacts on understory microclimate is inconclusive with respect to understory productivity, although it appears that blue oaks suppress grass productivity in more mesic environments while enhancing it (prolonging the growing season) in more xeric environments where the tree canopy can moderate the environmental extremes. Hydraulic lift by the blue oaks (Ishikawa and Bledsoe, 2000) has been observed as a means of providing the understory indirect access to deeper soil moisture, but its potential enhancement of understory productivity has not yet been quantified.

Time series of blue oak responses to climate are few, such that there is a dearth of data with respect to seasonal photosynthetic, transpiration, and physiological status under natural conditions. Griffin's (1973) 3-year monitoring of leaf water potentials in *Q. douglasii* and *Q. agrifolia* provides background on the tolerance limits of these species to soil moisture deficits. The sharp, monotonic decrease in leaf water potentials over the summer drought provides evidence that blue oak roots do not have deep access to the water table, but that these trees senesce in response to lack of water. Ishikawa and Bledsoe (2000) monitored soil moisture continuously over diurnal and seasonal cycles, discerning evidence of hydraulic lift by blue oaks.

Given the inconclusiveness of the ecological and biogeochemical studies on blue

oak, and the dearth of physiological data under natural conditions, this research helps to fill the gap by providing the first, continuous, full-year data set on the diurnal and seasonal water use, leaf physiological status, and accompanying meteorological drivers in a California blue oak canopy. Quantifying physiological responses to climate drivers will afford assessment of productivity limits on the system and hence help answer some questions about the potential for blue oak growth and regeneration. This data expands not only the database for California ecosystems in particular, but in general for Mediterranean ecosystems, and for savannas, for all of which there is limited data of this kind. Because the method used here for measuring sap flow has not been common for oaks, details on the measurement technique and interpretation with respect to oaks are provided here.

In differentiating the water usage of the vertical (tree/understory) and horizontal (open/below-tree canopy) structural components of a savanna, the following phenomena are quantified: the magnitudes of their fluxes, the seasonality of their partitioning of sensible and latent heat fluxes, seasonal trends in leaf water potential, tree canopy conductance and tree hydraulic conductivity, and responses of tree canopy conductance to climate drivers and soil moisture. The eddy covariance versus sap flow estimates of tree transpiration and conductance are compared. In analyzing the responses of transpiration and conductance to climate drivers and soil moisture, a modern regression technique is utilized to discern (rather than impose) non-linearities and interacting variables. Ultimately, it is discerned how the trees and herbaceous layer are coordinated to fully utilize available water and energy resources over their respective growing seasons, and discussion is made of the biophysical rationale for why the two different growth forms should coexist at their given coverage of the

landscape. This research also provides needed data for better understanding in particular of a threatened ecosystem type in California.

2.2 Study site

Measurements were conducted on a blue oak savanna in Ione, California (latitude: $38^{\circ} 26'$ N, longitude: $120^{\circ} 57' 30''$ W, elevation: 540'-580'). The landscape is characterized by flat terrain with a scattered, clumped distribution of blue oaks and a minority of grey pines over a continuous layer of Mediterranean annual grasses. The site is on a private ranch and is part of the AmeriFlux network of eddy covariance field sites (<http://public.ornl.gov/ameriflux>), and the site will henceforth be referred to as the Ione savanna site. The ranch is lightly grazed from the end of November to the beginning of June, with about 1 cow per 3-4 ha (70-100 cows for the 280 ha ranch). An accompanying site about 1 km across the road provided measurements on open grassland to aid in distinguishing the influence of the trees. Data for 2001 are presented here.

2.2.1 Climate and soils

The climate in Ione is Mediterranean, with cool, wet winters, and dry, hot summers, such that precipitation and temperature are seasonally out of phase with each other, with summer water deficits, as illustrated by the water balance for a typical year (Figure 2.1). Mean annual precipitation is 610 mm, and mean annual temperature is 16°C . Soils are Auburn series, Lithic haploxerepts, rocky loam, slightly acid, brown to yellowish red, and only 0.5-1.0 m deep above greenstone bedrock. Soil physical properties are given in

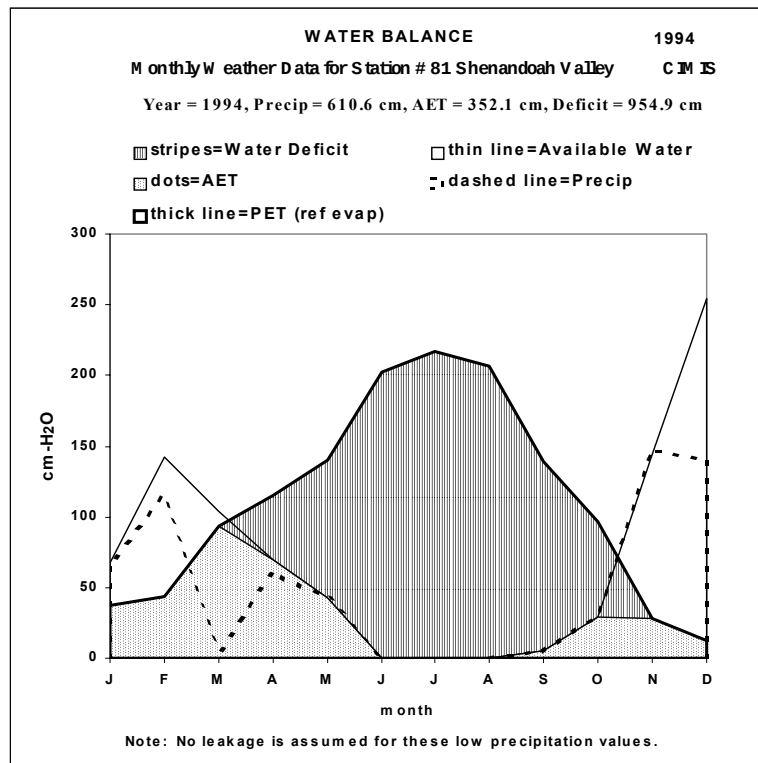


Figure 2.1: Water balance in Ione, CA, for 1994. Data from California Irrigation Management Information System (CIMIS). ET-evapotranspiration. Water deficit - amount of surplus energy that is not used in ET. Available water - water available for ET. AET - actual ET. PET - potential ET, a measure of available energy to perform ET.

Ione savanna loam soil	Measured				Saxton, et.al. (1986)			
	Sa/Si/Cl	ρ_{bulk}	θ_{sat}	θ_{min}	ρ_{bulk}	θ_{wilt}	θ_{FC}	θ_{sat}
	%	g cm^{-3}	vol frac		g cm^{-3}	vol frac		
tree canopy	38/45/18	1.58 ± 0.14	0.4	0.06	1.42	0.12	0.26	0.46
open	48/42/10	1.64 ± 0.11	0.4	0.06	1.52	0.09	0.23	0.42

Table 2.1: Measured soil texture, bulk density, and moisture levels at saturation and minimum field levels. Predictions of soil moisture critical points following Saxton, et.al. (1986). Ione, California, savanna site.

Table 2.1, which gives both values measured at the site by Xu (2002, unpublished) and predictions of soil moisture critical values based on models by Saxton, et.al. (1986). The values predicted from Saxton, et.al. (1986) serve primarily as a check for the field data. A soil moisture release curve by Xu (2002, unpublished) for this soil is available for relating soil water potentials and volumetric moisture (given later under Methods). There is an observable difference between soils found directly beneath the tree canopies versus in open areas. Soil bulk density is $1.58 \pm 0.14 \text{ g cm}^{-3}$ under the trees and $1.64 \pm 0.11 \text{ g cm}^{-3}$ in open grass areas between the trees.

Groundwater sources occur at 22 m and 104 m depths (Russell Tonzi, land owner, personal communication). The site is level, with maximum slopes in undulations of less than 15%.

2.2.2 Vegetation

The overall vegetation of the site consists of clumped blue oaks (*Quercus douglasii*, $\sim 190/\text{ha}$) with very few grey pines (*Pinus sabiniana*, $\sim 15/\text{ha}$), and a continuous layer of introduced Mediterranean annual grasses. The blue oaks are drought deciduous, leafing out in late March, and senescing continuously through the summer drought until full senescence

by November or December. The annual grasses sprout with the first winter rains, which can begin between November and the following January, then quickly senesce as the soil dries down during May. Thus, the oaks and the grass understory are out of phase in their growth seasons, with a short overlap during April when both are at their peak growth. Figure 2.2 shows the system in the early spring when the grasses are productive before the oaks have leafed out, and Figure 2.3 shows the system in the summer when the grasses have senesced while the oaks continue to be active. This difference in phenology provides an ideal system for differentiating the contributions of the under- and overstory to ecosystem exchanges of carbon dioxide, water vapor, and energy.

2.2.3 Tree characteristics

Stand characteristics of the blue oak and grey pine trees at the Ione savanna site are summarized in Table 2.2, as inventoried from a 1 ha area and along two 100 m transects. All trees within the 1 ha area and within 2 m on either side of the two transects were measured for diameter at breast height (dbh), and, of these, a total of 100 trees within the 1 ha quadrat were measured for height.

The tree density is the same as that observed by previous researchers for blue oaks on gentle slopes, where the upper limit of tree density is about 200/ha (Barbour and Minnich, 2000, citing Borchert, 1994, and Griffin, 1988). Tree dbh distribution, contribution of different size classes to total basal area, and the dbh-height relationship are shown in Figures 2.4 and 2.5. Unlike many blue oak sites where regeneration is commonly seen as a problem (Barbour and Minnich, 2000), this site has good representation of all age/size classes of the trees, with many saplings and 2-3 year old seedlings visible, indicating good



Figure 2.2: Blue oak and grey pine trees measured for sapflow, Ione savanna, early spring, March 24, 2001.



Figure 2.3: Blue oak and grey pine trees measured for sapflow, Ione savanna, summer, August 1, 2001.

Oak population		
age range	[years]	1-70
density	[number ha ⁻¹]	190
height	[m]	mode: 8.6, mean: 7.1, max: 13.0
diameter at breast height (dbh)	[cm]	mode: 22.1, mean: 19.9, max: 95.4
basal area	[m ² ha ⁻¹]	18.9
Pine population		
density	[number/ha]	3-24 (variable)
height	[m]	mean: 9.5
dbh	[cm]	mean: 25
All trees		
canopy cover (0.5 km scale)	[m ² /m ²]	0.39

Table 2.2: Stand characteristics of blue oak and grey pine trees at the Ione savanna.

regeneration. From tree cores, the oaks with 30 cm dbh are approximately 70 years old, such that, if extrapolation is done based on dbh, the oldest oak with a dbh of 77 cm is about 140 years old, which corresponds to the last regeneration episode observed for most blue oak stands, estimated to have occurred in the 1870's. The pine trees attain heights 2-3 m above the tallest oaks, but have a very low density, varying at the hectare scale from only 3 to 24 per hectare. Greater density of pines occurs in moister microsites, such as areas closer to seasonal streams and where oak density is also greater. The ranch owner at the Ione savanna actively manages the vegetation to prevent the encroachment of shrubs with herbicides, and the site is grazed in the late winter, as mentioned earlier. The site is thus very park-like, with no understory shrubs, one dominant tree species, blue oak, and one minor tree species, grey pine. Canopy cover of 0.39 was calculated from IKONOS imagery taken on June 2001, with canopy coverage calculated at a scale of 0.5 km x 0.5 km (Figure 2.6).

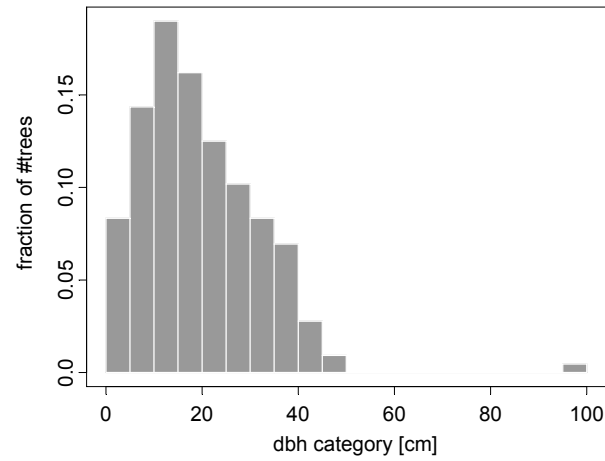


Figure 2.4: Fraction of blue oak trees per DBH size class, Ione savanna, California.

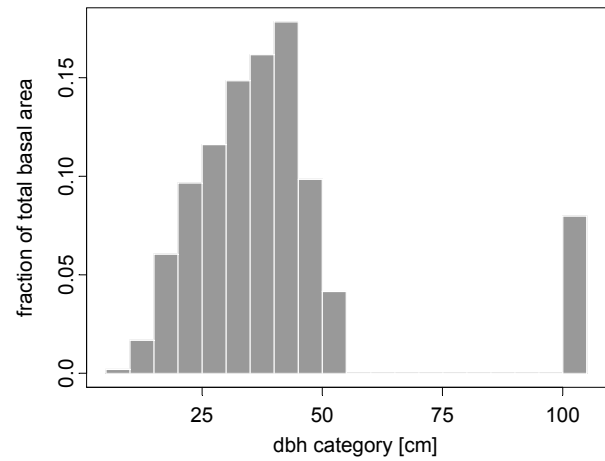


Figure 2.5: Contribution of blue oak DBH categories to total basal area, Ione savanna, California.

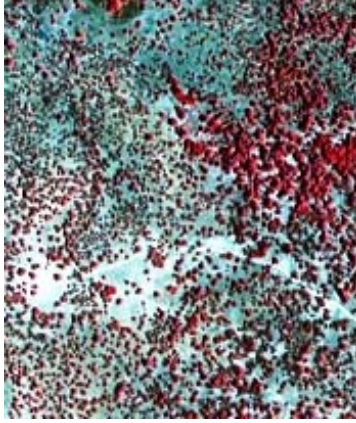


Figure 2.6: IKONOS satellite imagery of the Ione savanna site, June 2001. View is approximately 1.0 km x 0.8 km, with north up (see scale on topographic map figure).



Figure 2.7: Ione savanna site set-up, with north up. T - above-canopy tall eddy flux tower. U - understory eddy flux tower. S1 - sapflow set-up (data not used in this paper). S2 - sapflow set-up (data used in this paper). Grid squares are 100 m x 100 m; dashed line is a fence demarcating the property.

2.3 Methods

2.3.1 Meteorological and eddy covariance instrumentation

Meteorological variables and the fluxes of carbon dioxide, water vapor, and energy were monitored continuously on three different stations to differentiate open grass area, below-tree canopy, and whole-ecosystem exchanges, recorded on a half-hourly basis. A 2 m tower in an open grass area ("open" or "grassland") on the Ione grassland site commenced operation on October 24, 2000. A 2 m tower below the tree canopy ("understory" or "floor") on the Ione savanna site commenced on April 8, 2001. And a 20 m meteorological tower at approximately twice the maximum height of the oak canopy ("overstory" or "above-canopy" or "tall tower") on the Ione savanna commenced on May 7, 2001. The set-ups are diagrammed in Figure 2.7 (aerial view over a topographic map) and Figure 2.8 (conceptual horizontal view).

The meteorological variables monitored were air temperature (Vaisala, HMP-35A, platinum resistance thermometer in aspirated shield), relative humidity (Vaisala, HMP-35A, thin film capacitive polymer in aspirated shield), solar radiation (Kipp and Zonen pyranometer), photosynthetically active radiation (Kipp and Zonen PAR Lite), net radiation (Kipp and Zonen NR Lite), pressure (Vaisala PTB101B), precipitation (Texas Electronics, tipping bucket gauge), wind speed (Gill, WindMaster Pro sonic anemometer), soil temperature (lab-made thermocouple probes, three depth profiles at 2, 4, 8, 16, and 32 cm), soil heat flux (Hukseflux HFP01, three soil heat flux thermopile plates), and soil moisture (Delta-T, Theta probes, time domain reflectometry, two at 10 cm depth, two at 20 cm, and one at the soil surface). Tree bole temperatures were also measured by sap flow sensors

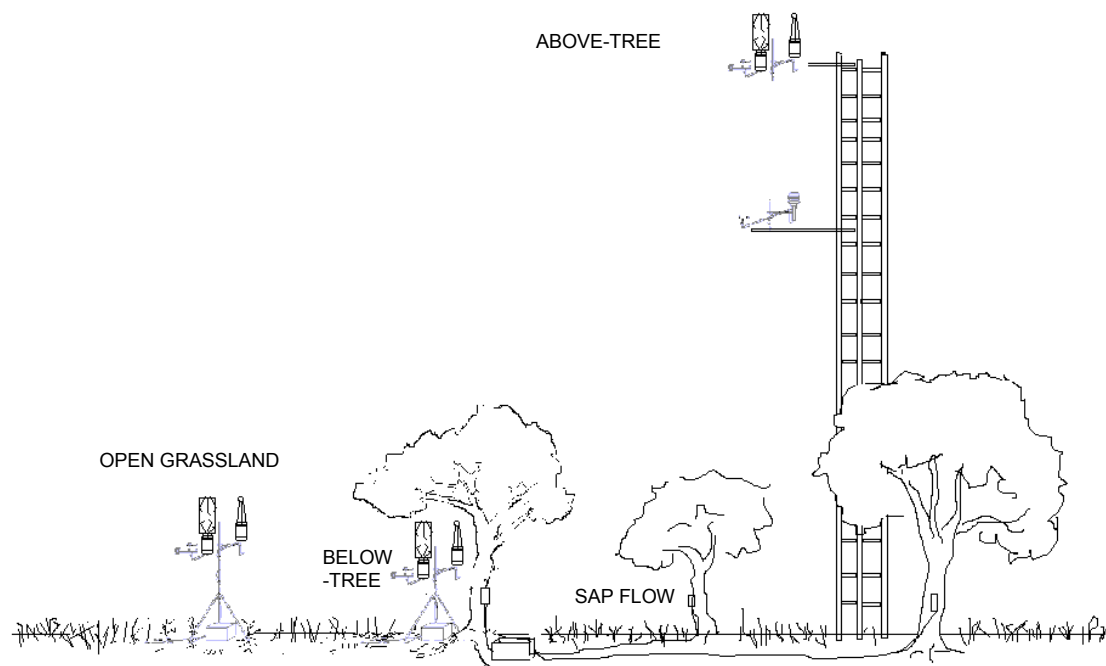


Figure 2.8: Diagram of Ione savanna and grassland instrumentation set-up for sap flow, eddy covariance, and meteorological measurements.

(described below), providing a means to estimate bole heat storage.

Fluxes of carbon dioxide, water vapor, and sensible heat were measured by the eddy covariance technique. The eddy covariance systems consisted of the Gill sonic anemometers to measure wind speed at 10 Hz, and open-path infrared gas analyzers (LI-7500, Li-COR) to measure water vapor and CO₂ concentrations. The theory of eddy covariance is described by Baldocchi, et.al. (1988), and the extent of its usage to monitor ecosystem exchanges is reviewed in Baldocchi, et.al. (2001). The technique has been seldom used beneath tree canopies, because still air or the disruption of the wind stream by local bluff bodies violate the conditions under which eddy covariance measurements are valid. However, for an open canopy like a savanna, the technique may be used to integrate over the forest floor environment as has been done under sparse canopies by Arneth, et.al. (1996), Baldocchi, et.al. (2000), and Wilson, et.al. (2001).

Soil moisture and relative extractable water (REW)

A variety of ways of representing soil moisture were examined, since different rationales exist for explaining plant responses to soil water availability. Soil moisture profiles were calculated in terms of potential (MPa) and in terms of volumetric relative extractable water content (REW), and depth-weighted averages of total soil moisture were calculated with regard to total soil depth and plant rooting depth.

Soil moisture potential (MPa) was calculated from the TDR profile measures of volumetric water content, and from soil moisture release curves for the Ione savanna soil

(Xu, 2002, unpublished):

$$\Psi_{soil} = -0.00483 * (\theta_{soil}^{-2.5656}) \quad (2.1)$$

where Ψ_{soil} [MPa] is soil water potential, and θ_{soil} [volume water / volume soil] is soil water content by volumetric fraction.

Relative extractable water (REW) is commonly calculated by other researchers (e.g. Granier, 1987) as:

$$REW = \frac{\theta_{soil} - \theta_{min}}{\theta_{FC} - \theta_{min}} \quad (2.2)$$

where θ_{min} [volume water / volume soil] is minimum observed soil water content (conceptually, this would best be the hygroscopic water content), and θ_{FC} [volume water / volume soil] is the soil water content at field capacity. To compare with concepts in ecohydrology, REW is calculated relative to the saturation point, rather than the field capacity, as is done by Rodriguez-Iturbe, et.al. (2000):

$$REW = \frac{\theta_{soil} - \theta_{min}}{\theta_{sat} - \theta_{min}} \quad (2.3)$$

To estimate θ_{min} , θ_{FC} , and θ_{sat} , observations of minimum and maximum soil moisture values from 2001 were used, checking against predictions of these moisture points by models of Saxton, et.al. (1986).

To estimate the average Ψ_{soil} or REW for the entire soil profile or as seen by the plant, the depth-weighted average of these values was calculated, interpolating between points.

2.3.2 Leaf area index and canopy cover

Leaf area index was estimated through three independent techniques to serve as checks on each other: optical measurements (LAI-2000, Li-Cor), allometric relations (Karlik, 2002, relations from harvests at another location), and litterfall (Battles, et.al., personal communication). Leaf area index is a critical parameter for numerous measures of ecosystem functioning, such as plant productivity, transpiration, and energy balance, but all measurement techniques are subject to a large amount of error: clumping violates canopy homogeneity assumptions for optical techniques (Ross, 1981; Chason, et.al., 1991; Baldocchi and Collineau, 1994; Chen, 1996); allometric relations may be population- or site-specific; and litterfall is subject to sampling errors.

Trends in tree leaf area index (LAI) were recorded from March-August 2001 through bi-weekly to monthly measurements with an LAI-2000 (Li-Cor) optical sensor along 3 radial, 200 m transects, at 2 m intervals along each transect. The transects consisted of one central transect extending from 50 to 250 m along the tall eddy flux tower daytime footprint, and two adjacent transects radiating 22.5° from the same origin west and east of the center transect. The LAI-2000 measurements were always made after dusk or before dawn on clear days in order to have homogeneous sky conditions. Due to the open nature of the canopy, this canopy structure violates the usual assumptions of homogeneity that are required for optical methods of measuring LAI (see Ross, 1981; Chen, 1996); also, the clumping of the trees prevents use of techniques for measuring individual tree LAI. Therefore, these optical measurements of LAI provide only a rough estimate and a means to monitor trends and describe spatial variability; the 2 m resolution is fine enough to

afford a statistical sampling for the purposes of areal averaging.

Leaf area was also estimated by dividing measurements of litterfall biomass by leaf specific weight. Litterfall was collected in 2001 by Battles, et.al. (unpublished), utilizing litter baskets both randomly placed and only under tree canopies. Leaf specific dry weight was sampled by Xu (unpublished) on a weekly basis during April-August 2001. Allometric relations for blue oak by Karlik (2002) were extrapolated to the Ione site as another independent estimate of LAI.

Tree canopy coverage was calculated from IKONOS satellite imagery of the site taken in June 2001 (Figure 2.6).

2.3.3 Sap flow

A total of 4 blue oak trees and 1 pine tree provided continuous, hourly sap flow data for 2001, using the heat pulse method (HPV). The sap flow from these trees were scaled up by population structure to stand transpiration, as has been done by several researchers for other species (scaling issues reviewed by Köstner, Granier and Cermák, 1998; temporal issues reviewed by Granier, et.al., 1996a; individual studies scaling to the stand level by Alsheimer, et.al., 1998; Arneth, et.al., 1996; Farrington, et.al., 1994; Granier, 1987; Granier and Loustau, 1994; Granier and Bréda, 1996; Hatton, et.al., 1995; Hogg, et.al., 1997; Köstner, et.al., 1998; Oren, et.al., 1998b; Saugier, et.al., 1997; Wullschleger, et.al., 2000b). Below are described in detail the sensor design, sampling scheme, and method of scaling tree transpiration to the stand scale.

Heat Pulse Velocity (HPV) Technique

The heat pulse velocity (HPV) method was used to measure sap flow, following a sensor design by Burgess, et.al. (2001). This method is based on measuring the difference in temperature rise up- and downstream of a heater probe that sends a short pulse of heat (usually 2-3 seconds) (Marshall, 1958; Swanson, 1962; Swanson and Whitfield, 1981; Swanson, 1994; Smith and Allen, 1996), diagrammed in Figure 2.9. The details of the equations used in calculating sap velocities may be read in Appendix E. The HPV method

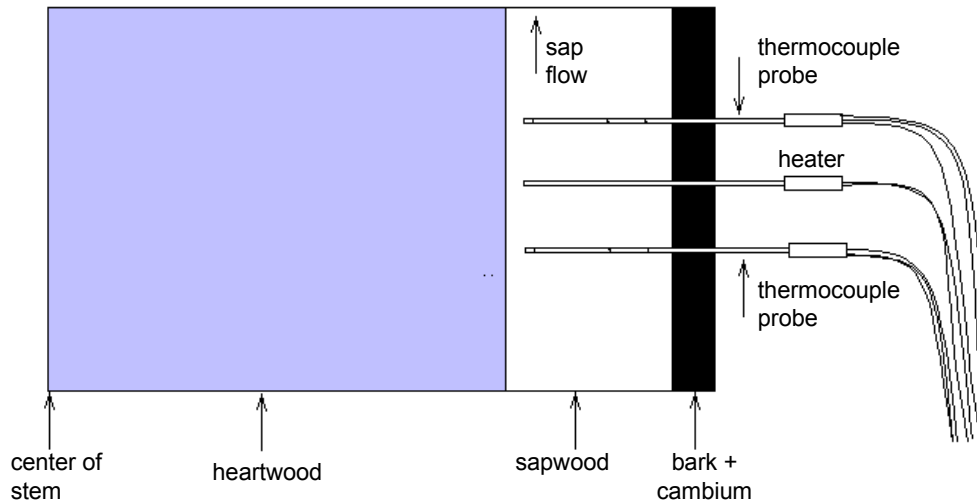


Figure 2.9: Diagram of heat pulse velocity (HPV) sensor for measuring sap flow.

was chosen instead of constant heat methods like those of Granier (1985) or Cermak, et. al. (1973), since the intermittent heat pulse requires less energy, the fine needle probes minimize damage to the tree, and the point measurement nature of HPV probes automatically provides quantification of radial profiles of sap velocity as well as resolution of low levels of

flow. In the Ione sensors, the sampling was at 3 different depths into the sapwood, inside the sapwood-bark boundary, and 1 cm and 2 cm into the sapwood, to capture the radial variation of sap flow. The upstream and downstream thermocouple probes were spaced equidistantly 0.6 cm from the central heater probe. The heater resistances were 14.5-16.6 Ohms, and 12V were applied for 2 seconds. Temperature traces were recorded at 0.5 Hz, 10 seconds before the onset of the heat pulse, and then for 2 minutes during and after the heat pulse. For calculation of heat pulse velocities from the heat ratio method, the temperature data from 70-110 seconds (at 0.5 Hz, 21 data points) were used. Each tree had one sensor at breast height (1.5 m) on the north side of the tree, to minimize the influence of diurnal bole temperature swings, and all sensors were insulated with styrofoam. Although it is known that the sap flow rate as well as volume can vary around the circumference of the tree due to asymmetries in the tree foliage and sapwood (Raschi, et.al., 1995; Tognetti, et.al., 1996), circumferential sampling was not done due to equipment capacity limitations, and it was assumed this detail would not provide better precision for scaling to the stand level. Temperature trace data were recorded once per hour.

During January 30-February 28, 2001, a diurnal cycle was downloaded on a weekly basis, and thereafter data were recorded continuously to provide an hourly record of sap flow. Since the blue oaks are leafless throughout the winter, these measurements provide a reference on how the sap flow sensors perform when no leaf transpiration should be occurring. A schematic of the wiring of a sap flow probe to the heater relay, multiplexer, and datalogger is given in Appendix E.

Tree population sampling

Two clusters of 5 trees were measured for sap flow, chosen to represent the range of dbh's of the population. A cluster of 5 oak trees, group S1, was monitored at a distance 100 m from the overstory tower within the tower daytime footprint, and a cluster of 4 oaks and 1 pine, group S2, were monitored at 200 m from overstory tower further upwind within the daytime footprint. The trees were selected to represent the basal area contribution of the trees within different size classes, as shown in Table 2.3. Basal area contribution rather than number of trees was used as the criterion, since the first more closely corresponds to contribution to total transpiration. One pine tree was included in the set of trees in S2. Data for 2001 are available only for the trees from setup S2, due to equipment malfunctioning at S1. However, the data here and previous work by Granier, et.al., 1996b, show that five trees are adequate for scaling to sap flow to stand-level transpiration when the sap flux densities are uniform among trees, as will be seen in the results. Note that there was no sap flow tree in the 50-100 cm dbh class, so data from the largest available tree was extrapolated to this class; the potential error in this extrapolation was considered not to be a significant problem, since the largest trees are small enough in population (only two trees of this size class found of 220 trees surveyed) to contribute only a small fraction of total sapwood area and hence a small fraction of fluxes (see again Figure 2.5). Each cluster of trees spanned an area about 30 m wide.

DBH class, cm	S1 100 m from tower DBH (Tree Tag)	S2 200 m from tower DBH (Tree Tag)	DBH class represented by S2
blue oaks			
10-20	15.1 (245)	19.2 (77)	0-20 cm
20-30	20.3 (248) 21.0 (252)		
30-40	35.2 (250)	30.6 (72) 30.5 (79)	20-40 cm
40-50	44.3 (255)	42.5 (71)	40-50 cm 50-100 cm
pine tree			
30 cm		29.8 (78)	

Table 2.3: DBH categories of sapflow trees.

Blue oak sapwood area

The sapwood area was calculated from a relation between dbh and sapwood area, derived from two available oak rounds, one 10 cm in diameter and the other 33 cm in diameter, giving a linear relation:

$$\text{sapwood area } [cm^2] = 0.22 * \text{dbh} [cm] \quad (2.4)$$

The relation between dbh and sapwood area is not necessarily intuitively linear, but given the few two samples, a linear relation is the only one that provided an intercept of zero. This rough, operational empirical relation is found to be adequate later.

Blue oak sapwood anatomy

In selecting a design for the sap flow sensors, it was necessary to consider complications arising due to the heterogeneous anatomy of oak trees, which are ring-porous.

Ring-porous trees, such as *Quercus*, *Fraxinus*, and *Carya*, have large-diameter xylem vessels in the early growing season and then smaller vessels toward the end of the growing season. By contrast, diffuse-porous trees, such as *Acer*, *Betula*, and *Populus*, have relatively small vessels interspersed uniformly through the sapwood (Nobel, 1991). Softwood trees such as *Pinus* have non-porous anatomy, having only tracheids and no vessels. Therefore, the more uniform anatomy of the latter two kinds of trees are easier to measure for sap flow, because all heat conductance techniques for measuring sap flow rely on assumption of sapwood homogeneity at some scale (see original theory by Marshall, 1958, and review by Swanson, 1994).

Blue oaks are characterized by seasonally varying xylem vessel diameter, so it was necessary to determine that vessel sizes were small enough in comparison to sap flow probe diameters to ensure an appropriate scale ratio in measuring heat conductance. Also, from previous work by Granier, et.al. (1996a) on oaks using different techniques, it is known that tyloses in older vessels reduce the hydraulic conductivity of the sapwood with radial depth; therefore, it was necessary to measure a radial profile of sap velocity. Blue oaks also have significant areas of ray cells that are not vertically conducting, so this areal fraction must be known when integrating sap velocities around the entire sapwood of the tree.

To measure xylem vessel diameters, radial trends, and ray cell areal coverage, thin sections were taken from a 10-cm diameter blue oak round. Since trees could not be cut down at the study site, the oak round was taken from the University of California Sierra Foothills Research and Extension Center (SFREC). Only one tree was sampled, so the variation is due to tree size or population is not known, but the measurements obtained at

least provide a rough estimate for this species. This round and also a bole section from a 30-cm diameter dead tree at the Ione savanna were used to estimate the relation of diameter to sapwood depth.

A thin section from the 10-cm diameter blue oak round from Sierra Foothills Research and Extension Center is shown in Figure 2.10. This image clearly shows the

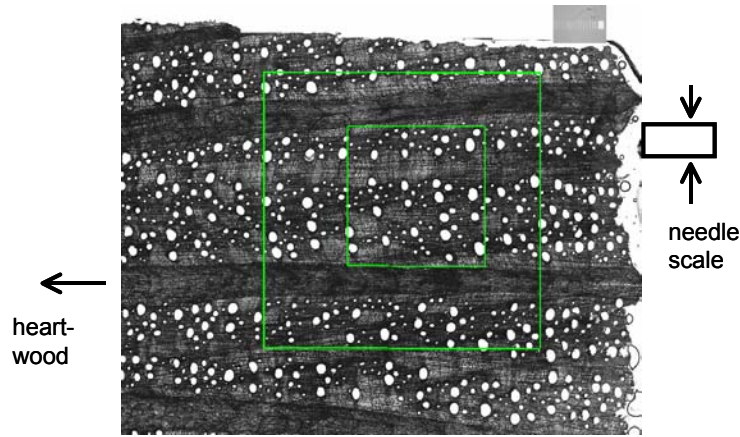


Figure 2.10: Blue oak bole thin section, cross section perpendicular to bole axis. Large box = 10 mm x 10 mm, small box = 5 mm x 5 mm. Needle scale is 1.275 mm.

seasonal variation in vessel size for this ring-porous tree, with larger, faster-conducting vessels during the early, wet growing season, and smaller vessels during the late, dry season. This particular image has the tyloses cleared in order to calculate vessel diameters. A close-up from this thin section in Figure 2.11 shows how the larger vessels are obstructed by tyloses in older annual rings. The dark areas of sapwood are ray cells, which are not vertically conducting and are significant enough in area to be necessary to account for when calculating conductive sapwood area. Only this one blue oak round was measured to provide approximate ranges of blue oak vessel sizes, densities, and ray cell coverage. It is not known what the level of variation could be between trees or populations, but the measurements

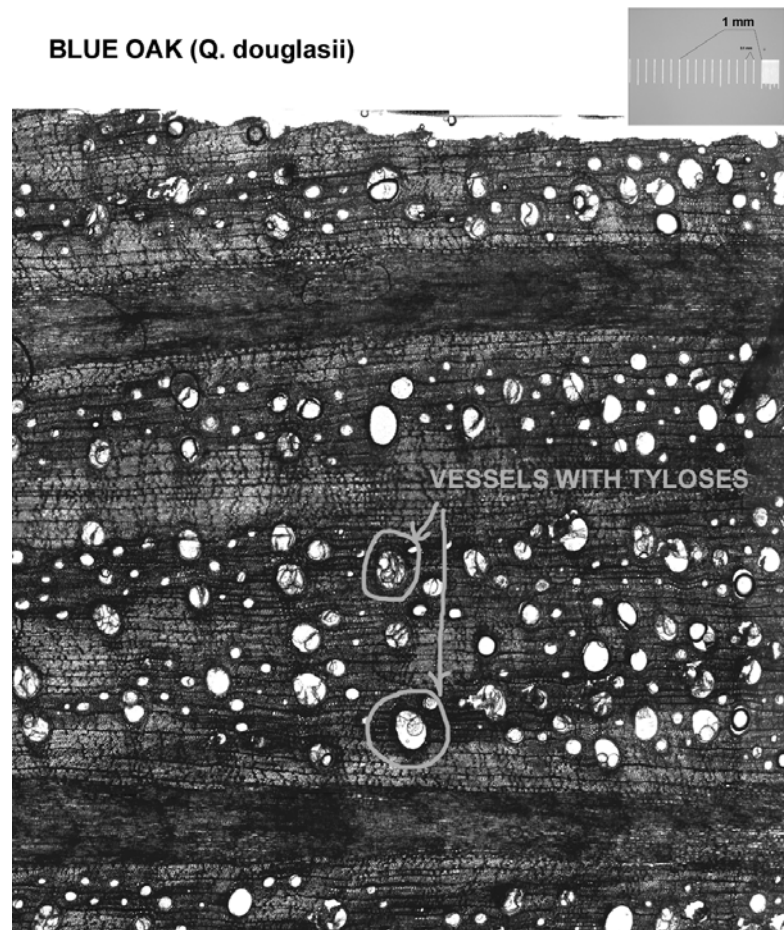


Figure 2.11: Blue oak (*Quercus douglasii*) thin section showing tyloses in larger vessels.

Ray cell areal fraction: 0.21
Vessel diameters:
range: 0.02-0.43 mm
median: 0.12 mm
Vessel areal fraction [mm^2/mm^2]:
of total area: 0.08
of non-ray cell area: 0.10
in total area: $3.2/\text{mm}^2$
in non-ray cell area: $4.1/\text{mm}^2$
Needle probe outer diameter: 1.275 mm
Distance between thermocouple junctions in needle: 10 mm

Table 2.4: Blue oak thin section measurements of ray cell area and vessel sizes.

derived from this sample provide an indication of the radial trends and magnitudes of sapwood components. Results are given in Table 2.4. The very maximum 0.43 mm size of the largest vessels, median size of 0.12 mm, and the distance between annual rings are small enough for a 1.3 mm diameter sap flow needle probe to average over an annual ring including two large and some small vessels in measuring heat conductance. Ideally, the vessels should be an order of magnitude smaller than the needle probe diameter, so the largest vessel size, 0.43 mm, may pose problems for this sensor design, as will be seen later. The median vessel size of 0.12 mm, on the other hand, is acceptable for assuming homogeneity within the scale of the needle diameter. A radial distance of 1 cm between measurement points is sufficiently far enough apart to distinguish radial trends in sap velocity.

Integrating heat pulse velocities to total tree sap flow

Sap flow for each measured tree was calculated following the method of Burgess, et.al. (2001): 1. Heat pulse velocities [cm hr^{-1}] were calculated using the heat ratio method, as described by Burgess, et.al. (2001), correcting for sensor misalignment and

wounding effects (details below). 2. Sap velocities [cm hr^{-1}] were calculated from heat pulse velocities based on saturated sapwood heat capacity. 3. At each hour, for each tree, sap velocities were interpolated linearly between measured points in the sapwood to obtain a radial trend in the velocities, assuming that the velocity is zero at the sapwood-heartwood boundary. 4. The radial trend in sap velocity was integrated around the entire sapwood area, and then multiplied by the percent area not covered by ray cells, thus obtaining the total sap flow rate for the tree (e.g. in cm^3/hr). Calculations here were done to account for the possibility of non-monotonic changes in sap velocity with depth into the sapwood, and the sometimes inconsistent variation in sap velocity radial trends will be addressed in discussion later. The details of the equations for calculating sap velocities and sap flow may be found in Appendix E.

The wood and sap physical properties used in calculating heat pulse and sap velocities are given in Table 2.5. All values are taken from the literature as noted in the table. For the thermal diffusivity, α , of wood parallel to the grain, a middle value of $2.5 \times 10^{-3} \text{cm}^2 \text{s}^{-1}$ was assumed between the extremes of $1.4 \times 10^{-3} \text{cm}^2 \text{s}^{-1}$ for water and $4.0 \times 10^{-3} \text{cm}^2 \text{s}^{-1}$ for dry wood (Burgess, et.al., 2001). Since thermal diffusivity of fresh wood declines with moisture content and tree bole soil moisture content can vary seasonally (swelling and shrinkage commonly observed from dendrometer bands, Zweifel, et.al., 2001), the seasonal trend in bole wood moisture content should be measured in order to track changes in α and most accurately calculate sap flow when using heat tracer techniques. Unfortunately, this parameter was not measured in 2001, so trends in estimated sap flow must be interpreted later in this light. Given that the oak vessel areal fraction over the

sapwood is 0.08, and assuming the woody matrix itself generally remains wet in fresh wood, the difference in thermal diffusivities between saturated sapwood and sapwood with dry or cavitared vessels could be as much as $0.2 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1}$, or an 8% difference from the chosen α .

Correction for sensor misalignment was done by solving for sensor alignment at times corresponding to zero sap flow rates in the trees. Since the trees could not be cut down, for the oaks, it was assumed that zero sap flow corresponded to nighttime (2:00 am) values in February 2001 when the oak trees were leafless, averaging the results for two different days. For the pine tree, mid-August, mid-day (13:00 pm) values were chosen, averaging also two days for the pine tree when the pine was experiencing water stress, low activity, and stomatal closure in the afternoon. This time of day in August was identified as the time of stomatal shutdown from inspecting the diurnal patterns of the heat pulse velocities over the full year of measurements, as this period produced the minimum sap flow values and was unlikely to be due to reverse flow during the dry season.

To correct for wounding effects, wound diameter was estimated for the oak trees to be the needle probe diameter (1.275 mm) plus twice the diameter of a largest blue oak xylem vessel (0.43 mm), giving a total 2.135 mm wound diameter. For the grey pine, the wound diameter value used was that found from sap flow measurements on Ponderosa pine at Blodgett Forest by Meredith Bauer (personal communication), who found the wound diameter to be 1.8 mm from dye techniques. Correction for the wound effect on measured heat pulse velocity was done using the numerical model of Burgess, et.al. (2001). Burgess, et.al. (2001) originally calculated their wound correction factor, the "B" factor, for time

courses 60-100 s after the heat pulse, while the time courses used here were slightly later, 70-110 s, to ensure strong linearity in the heat ratios with time. Therefore, the numerical wound correction model was re-calculated for the 70-110 s time range for a range of wound diameters of 1.7-2.2 mm. These new "B" factors are given in Table E.1 in Appendix E. The B value for the blue oak and grey pine wound diameters was obtained by linear interpolation between the values in Table E.1. This correction coefficient is multiplied by the mean heat pulse velocity over the given time range to give sap velocity. Note that since the wound diameter cannot really be determined more precisely than less than 0.1 mm, the potential error range in the wound correction factor is as follows. For the blue oak wound diameter of $2.14 \text{ mm} \pm 0.05 \text{ mm}$, the B factor range from linear interpolation is 1.9146 -1.6% or +1.7%, respectively. For the grey pine wound diameter of $1.8 \text{ mm} \pm 0.05 \text{ mm}$, the B factor range is 1.6832 -1.5% or +1.8%. If the uncertainty in the wound diameter is larger, say $\pm 0.1 \text{ mm}$, then the correction factor uncertainty approximately doubles these percentages. These are the potential percent errors in sap velocity with respect to estimating the wound effect.

If data were missing at a radial depth for a particular hour, the sap velocities for the adjacent radial depths were interpolated over the missing point.

Scaling tree sap flow to stand transpiration

To scale the individual tree sap flow measurements to obtain stand transpiration [cm hr^{-1}], the following procedure was used: 1. The sap flow rate [$\text{cm}^3 \text{ hr}^{-1}$] for a tree was linearly scaled by the mean sapwood area for its dbh class. 2. Sap flow rates were then interpolated for all dbh classes between the measured rates, giving a predictive curve

Parameter	Units	Value	Source
α , thermal diffusivity of fresh, green wood	$[\text{cm}^2\text{s}^{-1}]$	0.0025	Burgess, et.al. (2001)
ρ_{wood} , density of wet woody cell wall	$[\text{kg m}^{-3}]$	1530	Panshin and deZeeuw (1980)
ρ_{sap} , sap density, same as water	$[\text{kg m}^{-3}]$	996	Mills (1999)
$c_{p,wood}$, dry wood specific heat	$[\text{J kg}^{-1} \text{K}^{-1}]$	1200	Burgess, et. al. (2001)
$c_{p,sap}$, sap specific heat, same as water	$[\text{J kg}^{-1} \text{K}^{-1}]$	4178	Mills (1999)
Φ_{sat} , saturated wood moisture content	$[\text{m}^3 \text{m}^{-3}]$	0.7	S. Burgess, personal communication

Table 2.5: Wood physical and thermal parameters

for sap flow rate by dbh class. 3. The sap flux density (tree sap flow rate divided by tree sapwood area) for a dbh class, f_{dbh} $[\text{cm hr}^{-1}]$, was then multiplied by the sapwood area density for a dbh class, n_{dbh} $[\text{m}^2 \text{m}^{-2}]$, and all classes summed to obtain the stand-level transpiration rate, T_{stand} $[\text{cm hr}^{-1}]$:

$$T_{\text{stand}} = \sum_{dbh} f_{dbh} \cdot n_{dbh} \quad (2.5)$$

Filling missing hourly data was not done when performing daily sums of transpiration, but missing data was indirectly accounted for by merely scaling the daily average to 24 hours.

If more than one half of a day's data were missing, no daily sum was calculated.

The sap velocity and sap flux density are most important for understanding how tree anatomy influences sap flow, detecting errors in measurement technique with regard to radial and circumferential variation in the tree, and investigating variation between trees of different size, age, or canopy position. Note that sap velocity can only be obtained from the heat pulse technique, which measures point-wise velocity, whereas another popular sap flow technique by Granier (1985) is based on average flux densities. Sap flux density is

more commonly an intermediary calculation for scaling to stand-level transpiration, and sometimes sap flux density is calculated as per projected crown area rather than per sapwood area (Arneth, et.al., 1996; Wullschleger, et. al., 2000b). The reader is advised to distinguish between *sap velocity* (the absolute speed at which the sap is moving upward through xylem vessels), *sap flux density* (the flux distributed over the sapwood area), and *stand transpiration* as all three are in units of cm hr^{-1} or length per time. Note that the sap flow literature has not yet developed standard units of measure with respect to preferred length, mass, and time scales (issues reviewed by Edwards, et.al., 1997). The earlier literature in the development of the heat pulse technique (Hüber and Schmidt, 1937; Marshall, 1958; Swanson, 1962; Swanson and Whitfield, 1981) used velocity units of cm hr^{-1} , while more recently researchers have begun to convert to SI units of mm s^{-1} . For flux density, both length per time, volume per area per time (length cubed or liters, per area per time) and mass (g or kg, less commonly moles) per time are used, with intercomparisons seldom being done among species in most studies. Stand transpiration is more commonly analyzed in units of mm hr^{-1} and mm day^{-1} . Data are provided in the commonly used units for both early and recent literature, generally considering metric length units to be easily interconvertible by the reader.

2.3.4 Leaf water potential

Leaf water potential was measured in order to obtain an integrative quantification of the soil moisture available to the trees over time (Ritchie and Hinckley, 1975) and to calculate tree hydraulic conductivity in conjunction with other measurements. The sap flow trees were all measured for both pre-dawn and mid-day leaf water potential every

two weeks during April 26-August 1, 2001. Two leaves were clipped from each tree and immediately measured in a Scholander pressure bomb. One pre-dawn to dusk sequence of measurements was made on 3 sap flow trees in June 2001, clipping 2-3 leaves from each tree every two hours.

2.3.5 Tree hydraulic conductivity

Tree hydraulic conductivity, k_{tree} , was calculated in order to discern its potential constraints on tree transpiration in addition to stomatal resistance and to see how the conductivity changes seasonally. Tree hydraulic conductivity is defined here as the conductivity of water of the tree through the roots to the leaf mesophyll, or the inverse of the whole-tree resistance relative to water potentials between the soil and the leaf interstitial spaces. This conductivity therefore is a measure through all the plant tissues, generally meaning the stems, and excluding the leaf stomates. The details of issues regarding hydraulic architecture and conductivity were reviewed in Chapter 1, with a brief re-cap here. The tree hydraulic conductivity is an important but difficult to quantify bulk measure for characterizing tree water transport relative to soil moisture access. Researchers have attempted to quantify it through laborious lab measurements of saturated flow of water through cut stems (e.g. Tyree, et.al., 1993b), or by solving for the conductance from water potentials and sap flow measured in the field (Anfodillo, et.al., 1998). It can be used for interpreting tree morphology, particularly the constraint of water transport on tree height (e.g. Becker, et.al., 2000; Dawson, 1998, fog sources for tall redwoods). Also, it is a simple bulk value to approximate the details of tree hydraulic architecture, which are difficult to measure and represent in models (reviews by Sperry, 2000, and Meinzer, et.al., 2001, on

research issues; Jackson, et.al. 2000 on root uptake). Detailed models of root uptake (e.g. Nobel and Alm, 1993) and sap transport (most advanced, Fröh and Kurth, 1999) simulating branching and internal wood anatomy give insight into the physical mechanisms of water movement through the plant, but are too computationally and parameter-intensive to broadly apply for predicting canopy-level transpiration. A resistance-based model like that of Williams, et.al. (1996) uses bulk tree hydraulic conductivity parameterized in a layered scheme, relying on previous detailed harvest data by Tyree, et.al. (1993b). Tree hydraulic conductivity may eventually serve as a rough link between plant ecophysiology and hydrology to introduce the role of vegetation into hydrological models of soil water balance.

It should be noted that using fluxes measured in the field to assess tree hydraulic conductivity must include the stomatal conductance as part of the overall tree conductivity. Also, the conductivity is not constant, but is dependent on the sapwood water content and the occurrence of embolisms. Therefore, this definition of whole-tree conductivity is variable, dependent on environmental and plant physiological condition. Recognizing that this is a rough, bulk measure of the ability of trees to transport water from the soil to the leaves, it can nonetheless still serve as a useful indicator for drawing comparisons between species or between seasons.

The tree hydraulic conductance was calculated from transpiration and leaf water potential measurements (with appropriate caveats that this is back-of-the-envelope type of calculation for the purpose of comparing trends). Again, the calculation below is not adequate for discerning physiological mechanisms along the hydraulic pathway, but it may

serve as a rule of thumb for canopy-level transpiration estimates or to compare trends among individual trees. Recall that the leaf mesophyll provides the supply of water to the leaf while the stomates control the loss, such that they form a budget of leaf interstitial water content (Equation 4.7a, leaf water budget):

$$l_i \frac{dW_i}{dt} = E_{mesophyll} - E_{leaf} \quad (2.6)$$

$$= k_{tree} (\Psi_{leaf} - \Psi_{soil}) - g_{leaf} \cdot VPD \quad (2.7)$$

(Here, g_{leaf} incorporates both boundary-layer and stomatal conductances for simplicity, as this section focuses on the tree internal conductivity). Or, alternatively, one can observe that the tree hydraulic resistance and leaf resistance are in series, such that the total resistance between the soil and the atmosphere is:

$$1/g_{tot} = VPD/E_{leaf} + (\Psi_{leaf} - \Psi_{soil})/E_{mesophyll} \quad (2.8)$$

Hydraulic conductivity, k_{tree} , for each individual sap flow tree was calculated for days on which both pre-dawn and mid-day leaf water potentials and sap flow were measured. The k_{tree} was solved for by assuming that $E_{mesophyll}$ is equal to sap flow, F , using pre-dawn leaf water potential, $\Psi_{leaf,pre-dawn}$ as an approximation of soil water potential, and mid-day leaf water potential, $\Psi_{leaf,mid-day}$ as the leaf driving potential for sap flow, F .

$$E_{mesophyll} = F_{mid-day} = k_{tree} (\Psi_{leaf,mid-day} - \Psi_{leaf,pre-dawn}) \quad (2.9)$$

where:

$$\begin{aligned} F_{mid-day} &= \text{tree sap flow at mid-day } [\text{cm}^3 \text{ hr}^{-1}] \\ k_{tree} &= \text{tree hydraulic conductance } [\text{cm}^3 \text{ hr}^{-1} \text{ MPa}^{-1}] \\ \Psi_{leaf,mid-day} &= \text{leaf water potential at mid-day } [\text{MPa}] \\ \Psi_{leaf,pre-dawn} &= \text{leaf water potential at pre-dawn } [\text{MPa}] \end{aligned}$$

Note that the pre-dawn leaf water potential may not equilibrate to the concurrent soil water potential due to nighttime transpiration (Donovan, et.al., 2001) or poor soil-root hydraulic conductivity, but the pre-dawn values do at least provide a measure of temporal trends in the soil moisture that is available to the plants.

Because sap flow lags leaf transpiration and hence leaf water potential, and because the mid-day leaf water potential is an integration of the activity since pre-dawn, and since some hours of sap flow data were missing on three days that leaf water potential was measured, $F_{mid-day}$ was taken as the morning averages (9:00-12:00 am PST) of the sap flow of the previous, concurrent, and following days that leaf water potentials were measured. The hours of 9:00-12:00 were chosen, since these hours correspond to times of peak flow during the day when the stomata are not closed. Diurnal cycles were inspected to ensure that there were no weather anomalies on the three consecutive days, such that all three days exhibited similar climatic conditions.

2.3.6 Tree canopy conductance

The tree canopy conductance was calculated from both eddy flux and sap flow data. This conductance is a critical measure for predicting fluxes from plant canopies, and separating the tree layer from the understory layer as well as relating to meteorological drivers has seldom been done thoroughly by previous researchers (as reviewed in the introduction to this section). Tree transpiration from the eddy flux data was estimated by subtracting the understory and open grassland fluxes (apportioned by fraction of canopy cover) from the overstory tower fluxes. For the sap flow data, the conductance could only roughly be approximated, since sap flow is a smoothed and lagged expression of actual

transpiration at the hourly time scale. Since sap flow lags transpiration by 1-3 hours (Goulden and Field, 1994), the meteorological drivers of 2 hours earlier were used to invert from the sap flow data. Tree canopy conductance was calculated by inverting the Penman-Monteith equation (Thom, 1975; Kelliher, et.al., 1995) on tree-only fluxes (note that tree transpiration, $E_{veg,tree}$ is expressed in m s^{-1} rather than the common units of $\text{kg m}^{-2} \text{ s}^{-1}$):

$$E_{veg,tree} = \frac{s_{vap} (\Phi_{net} - \mathcal{G}_{soil} - \mathcal{G}_{bole} - \mathcal{G}_{air,heat} - \mathcal{G}_{air,LE}) + \rho_a c_p G_{aH} VPD}{\rho_{H_2O} \lambda_{LE} (s_{vap} + \gamma G_H / G_V)} \quad (2.10)$$

where:

- $E_{veg,tree}$ = tree canopy transpiration [m s^{-1}]
- s_{vap} = slope of the saturation vapor pressure curve, de_{sat}/dT [Pa K^{-1}]
- Φ_{net} = net radiation for tree canopy cover [W m^{-2}]
- $\mathcal{G}_{soil}$ = soil heat flux [W m^{-2}]
- $\mathcal{G}_{bole}$ = tree bole heat storage [W m^{-2}]
- $\mathcal{G}_{air,heat}$ = canopy air space heat storage [W m^{-2}]
- $\mathcal{G}_{air,LE}$ = canopy air space latent heat storage [W m^{-2}]
- ρ_a = density of dry air [kg m^{-3}]
- c_p = specific heat capacity of air, 1012 [$\text{J kg}^{-1} \text{ K}^{-1}$]
- γ = psychrometer constant [Pa K^{-1}]
- G_{aH} = canopy aerodynamic conductance of heat [m s^{-1}]
- G_V = canopy conductance of water vapor [m s^{-1}]
- λ_{LE} = latent heat of vaporization, 2.454×10^6 [J kg^{-1}] at 20 °C
- ρ_{H_2O} = density of liquid water [kg m^{-3}]

Solving for G_V gives:

$$G_V = \frac{\gamma G_{aH} \rho_{H_2O} \lambda_{LE} E_{veg,tree}}{s_{vap} (\Phi_{net} - \mathcal{G}_{soil}) + \rho_a c_p G_{aH} VPD - s_{vap} \rho_{H_2O} \lambda_{LE} E_{veg,tree}} \quad (2.11)$$

This representation gives a bulk tree canopy conductance per land area, viewing the trees as a sparse "big leaf." G_V can then be separated into its serial surface resistance and boundary layer resistance components $\left(\frac{1}{G_V} = \frac{1}{G_s} + \frac{1}{G_{aV}}\right)$, and be scaled to obtain measures with respect to leaf area, $G_{V,s}$, or canopy cover, $G_{V,cc}$, for comparison to other literature values. Since the tree-only latent energy fluxes from measurements could be used, this inversion does not require distinguishing resistances of the open grass and tree canopy

areas, as would be done for dual source models geared toward predicting full-system fluxes (Lhomme and Chehbouni, 1999; Kustas and Norman, 1999ab; Dolman, 1993; Shuttleworth and Wallace, 1985).

The **aerodynamic conductance of heat**, G_{aH} , is a function of wind speed and is calculated for homogeneous closed canopies (Jones, 1992; Campbell and Norman, 1998) as:

$$G_{aH} = \frac{k^2 u_z}{\left[\ln \left(\frac{z-d}{z_{0M}} \right) + \Psi_M \right] \left[\ln \left(\frac{z-d}{z_{0H}} \right) + \Psi_H \right]} \quad (2.12)$$

where $k \approx 0.41$ is the von Karman constant; u_z is the wind speed at height z above the canopy; d is the zero plane displacement; z_{0M} and z_{0H} are the roughness lengths for momentum and heat, respectively; and Ψ_M and Ψ_H are the diabatic stability corrections for momentum and heat flux, respectively. For sparse canopies, this equation can be used with the appropriate adjustments for the roughness lengths (see below).

Under neutral conditions, Ψ_M and Ψ_H are simply zero, but under unstable conditions, various empirical curves have been formulated from data. Calculated conductance was simply calculated during neutral conditions (for obtaining climatic response functions later), so it was unnecessary for to correct for instability in this case.

Wind profiles were not measured at the Ione savanna site yet in 2001, so values of d and z_{0M} were estimated from the literature. Raupach (1994) derived simple relations for d and z_{0M} relative to canopy height, h , and area index, fitted to field and wind tunnel data. Raupach notes that these relations simplify out the distribution of canopy density, but that further such detail requires knowledge of much less available parameters. Miranda, et.al. (1997) conducted eddy covariance measurements over Brazilian cerrado, where their

tree canopy LAI ranged from 0.4 to 1.0 between the dry and wet seasons, with a mean height, h , of 9 m. Their wind profile measurements yield the relations $d = 0.7h$ and $z_{0M} = 0.13h$, which correspond to the data fit by Raupach (1994) and the range of values compiled by Monteith and Unsworth (1990) ($d/h = 0.6 - 0.7$, $z_{0M}/h = 0.08 - 0.12$), but with the momentum roughness length enhanced, as is expected for a sparse canopy. Their LAI range is the same for the Ione blue oak site between the winter and summer, while the Ione tree canopy height averages 7 m for the oaks. Given the similarity in canopy structure between the Ione and Brazil sites, Miranda, et.al.'s (1997) relations for d and z_{0M} are used here. Therefore, this gives the Ione site $d = 4.9$ m, $z_{0M} = 0.9$ m.

For homogeneous canopies, the roughness length for heat, z_{0H} , is normally obtained by similiarity with the roughness length for momentum after work by Garratt and Hicks (1973):

$$\ln \left(\frac{z_{0M}}{z_{0H}} \right) \approx 2 \quad (2.13)$$

For sparse canopies, the above simple relationship for roughness lengths does not necessarily hold, but the ratio can be much larger. In this case, the momentum flux increases due to bluff body effects, but the sensible heat flux does not similarly increase, because the sources and sinks of sensible and latent heat may not be the same (Blyth and Dolman, 1995; Van den Hurk and Holtslag, 1997). Also, the roughness length for heat, z_{0H} , varies with humidity deficit and available energy (Blyth and Dolman, 1995). Dolman's (1993) dual-source model for the HAPEX-Sahel campaign over a tiger bush savanna found an order-of-magnitude difference between the roughness lengths for heat for homogeneous vs. sparse canopies. For a canopy 2-3 m high, the sparse value of z_{0H} is 20-30 times smaller than

the homogeneous value (Blyth and Dolman, 1995). This is still a rough range, but is the best empirical evidence for a savanna-type of ecosystem thus far; therefore, the mid-value of 25 is used as a scaling factor to obtain heat roughness length from momentum roughness length:

$$z_{0H} = \frac{z_{0M}}{25} \quad (2.14)$$

With the lone value of $z_{0M} = 0.9 \text{ m}$, this gives $z_{0H} = 0.04 \text{ m}$.

Net radiation for the trees was calculated from the difference between the over-story eddy covariance tower net radiation and the understory tower flux measurements. The understory net radiation was estimated through the energy balance, in which the net radiation should equal the sum of the sensible (H), latent (LE), and soil heat (G) fluxes. This estimate of understory net radiation from flux measurements is considered preferable to that measured by a net radiometer below the canopy, because the eddy covariance measurements cover a larger footprint than a net radiometer would. Therefore:

$$R_{net,trees} = R_{net,above-tree} - R_{net,understory} \quad (2.15)$$

$$= R_{net,above-tree} - (H_{understory} + LE_{understory} + G_{soil}) \quad (2.16)$$

Bole heat storage, $\mathcal{G}_{bole}$, was calculated in W m^{-2} land area from the radial temperature profiles from the sap flow sensors and then scaling up over the estimated surface area of the tree boles within a stand. The heat flux into a bole, g_{bole} , was simply:

$$g_{bole} = -k_{wood} \frac{dT_{bole}}{dr} \quad (2.17)$$

where k_{wood} = thermal conductivity of fresh wood perpendicular to the grain, $0.21 \text{ W m}^{-1} \text{ K}^{-1}$ (Mills, 1999); T_{bole} is the bole temperature as measured by the sap flow sensors; and r

is the radial distance into the tree bole. The temperature difference used was that between the innermost and outermost temperature sensors, which were 2 cm apart, and averages were done of the heat flux values calculated from the upper and lower sensors in the tree. The surface area of a tree, A_{bole,dbh_i} , was calculated as the surface area of a cone, and the heat flux was simply extrapolated over this surface. Total heat flux was scaled up to the stand scale by population density by diameter size class, n_{dbh_i} , and then the total heat flux was normalized by ground area.

$$\mathcal{G}_{bole}(t) = \sum_{dbh_i} n_{dbh_i} \cdot g_{bole,dbh_i}(t) \cdot A_{bole,dbh_i} \quad (2.18)$$

Air heat storage, $\mathcal{G}_{air,heat}$, was calculated by using the temperature profiles from the soil, understory eddy flux tower, and above-canopy tall eddy flux tower. Heat storage was calculated from the time difference in air temperatures at these points, linearly interpolating the time changes between height points, z , and integrating the point-wise heat storage from the ground to the tall tower height, z_{ref} :

$$\mathcal{G}_{air,heat}(t) = \int_0^{z_{ref}} \rho_{air}(t, z) c_{p,air}(t, z) \frac{dT_{air}(t, z)}{dt} dz \quad (2.19)$$

The density, ρ_{air} , and heat capacity, $c_{p,air}$, of air were calculated to take into account variation in temperature and humidity. Since taking the time differences gave mid-point values between times of the other measurements, such that the air heat storage values corresponded to 15 minutes in between the half-hourly meteorological measurements, the air heat storage values were linearly interpolated back to the times of day corresponding to the eddy flux and meteorological measurements to allow simultaneous calculations using all variables of interest.

Similarly, **latent heat storage** in the canopy air space was calculated based on the time change in absolute humidity:

$$\mathcal{G}_{air,LE}(t) = \int_0^{z_{ref}} \lambda_{LE} MW_{H_2O} \frac{d\hat{\rho}_{air}(t, z)}{dt} dz \quad (2.20)$$

2.3.7 Response functions

Statistical analysis was done to identify responses of G_V to environmental drivers. Rather than fit the individual drivers to curves based on previous theory of responses, a diagnostic technique was used, the Alternating Conditional Expectations algorithm of Breiman and Friedman (1985) to discern non-linear behaviors in the data itself, and only then formulated a statistical model that best describes the data. More details are provided below. The goal is not to obtain an empirical predictive model but to discern important qualities of this blue oak system from the data, identify non-linear responses and significant asymptotes or optima, particularly with respect to the impact of soil moisture deficit on conductance, and to compare to values in other ecosystems. Obviously, the conductances G_V as calculated from inverting the Penman-Monteith equation are directly functions of the variables used to do that inversion, namely available energy, vapor pressure deficit, pressure, wind speed, air temperature, and latent energy fluxes. However, one cannot discern the response of G_V to additional drivers that are not included in the Penman-Monteith equation and which influence latent energy fluxes, such as soil moisture, light, and variables that affect simply the measurement technique, such as wind speed or temperature. Therefore, a statistical analysis is a means to identify the significant system responses to all these individual drivers. In the analysis here, a modern technique is used for discerning the

patterns of non-linear responses of G_V to environmental variables, rather than imposing response curve forms beforehand. This technique is elaborated below.

To review, for statistical modeling of conductance, many researchers have followed the modeling work of Jarvis, et.al. (1976), modeling stomatal or canopy conductance as a simple multiplicative model of non-linear response functions or "stress factors" that are assumed independent, scaled between 0 and 1, which reduce the conductance below its maximum:

$$g_s = g_0 \cdot f_{T_a}(T_a) \cdot f_{PAR}(PAR) \cdot f_{VPD}(VPD) \cdot f_{\Psi}(\Psi) \cdot f_{other}(other) \quad (2.21)$$

Here, g_0 is maximum stomatal conductance, T_a is air temperature, PAR is photosynthetically active radiation, VPD is vapor pressure deficit, and "other" could be such potentially influential variables as wind speed, leaf area index, carbon dioxide concentration, or soil moisture deficit. Jarvis, et.al. (1976) originally developed this framework for leaf conductances, and then applied it to crops (Jarvis, et.al., 1981). This model then was extended for natural canopies (Stewart, 1988; Stewart and Gray, 1989), such that now it has become common for researchers to derive response functions at the canopy scale. This simple model is very useful for operational empirical predictions of conductance, but its form is an artificial construct with no actual theoretical, mechanistic basis. To obtain a fit of this type of model to their particular ecosystem, investigators will generally perform preliminary data inspections for non-linearities by simply plotting the environmental variable versus the conductance, sometimes in a step-wise fashion to attempt to account for other simultaneously varying environmental drivers (e.g. Granier and Loustau, 1994; Granier and Breda, 1996; Filho, et.al., 1998). This practice may not uncover the relations between the vari-

ables if there is too much confounding variability obscuring individual patterns. The data are then forced into a statistical model that may not offer the best fit or description of that data. Modern advanced statistical algorithms arose during the mid- to late 1980's for revealing non-linear responses in multivariate data (rather than merely fitting to given response forms) and have been used as diagnostic techniques by researchers more recently.

The Alternating Conditional Expectations (ACE) algorithm (Breiman and Friedman, 1985) was used to detect non-linear relations *a priori*. This is one of many possible statistical fitting algorithms that are useful as diagnostics for detecting non-linear responses in statistical models (e.g. AVAS, additivity and variance stabilising transformation of Tibshirani, 1988). ACE is an iterative algorithm that seeks to maximize correlation between the predictor and the response in a least-squares regression without imposing prior assumptions about their non-linearities. Unparameterized transformations from this algorithm result in an additive model of the data, to which smooth functions can be fit to approximate the forms of the transformations. Regressions run on these transformations then provide measures of the improvement in goodness of fit provided by the fits to the non-linearities, as is expanded on below.

The Jarvis model can be transformed from a multiplicative model to an additive model by taking its logarithm:

$$\begin{aligned} \ln(g_s) = \ln(g_0) + \ln(f_{T_a}(T_a)) + \ln(f_{PAR}(PAR)) + \ln(f_{VPD}(VPD)) + \ln(f_{\Psi}(\Psi)) \\ + \ln(f_{other}(other)) \quad (2.22) \end{aligned}$$

Regressions on this additive model can then be performed to discern the forms of the response functions by examining, for example, the partial residuals with respect to each

variable. However, it should be noted that, in general, the Jarvis model is primarily an expedient and theoretical formulation, and real data may not fit this log-linear form. A more general approach is simply to consider other possible transformations, t_X :

$$t_{g_s}(g_s) = t_{g_0}(g_0) + t_{T_a}(f_{T_a}(T_a)) + t_{PAR}(f_{PAR}(PAR)) + t_{VPD}(f_{VPD}(VPD)) + t_{\Psi}(f_{\Psi}(\Psi)) \\ + t_{other}(f_{other}(other)) \quad (2.23)$$

where the t_X are unspecified transformations for each variable X . If t_{g_s} is the natural log, then the result is a log-normal model that can be transformed into the multiplicative form of a Jarvis model to derive the functions f_X . If t_{g_s} is some other transformation than log, then the problem can simplify to direct transformations on all variables, which is just a Generalized Additive Model (GAM):

$$t_{g_s}(g_s) = t_{g_0}(g_0) + t_{T_a}(T_a) + t_{PAR}(PAR) + t_{VPD}(VPD) + t_{\Psi}(\Psi) + t_{other}(other) \quad (2.24)$$

The data of canopy conductance were modeled using this most general form.

To assess the shape of these response functions from data, the canopy conductance of water vapor, G_V , was first calculated by inverting the Penman-Monteith equation, as described in the section above. Then diagnostics of the data were run with the Alternating Conditional Expectations (ACE) algorithm (Breiman and Friedman, 1985; S-Plus statistical software, MathSoft)) to discern non-linear relations between the driving variables and the conductance response. Curves were then fit to the resulting ACE transformations for the response of G_V to driving variables. Analysis of variance with the Chi-squared test between a null linear model and the model with non-linear transformations provided confidences in the improvement in goodness of fit by the latter. The most significant

explanatory variables and interaction terms were saved into a final terse model. Among the driving variables investigated were: air temperature, vapor pressure deficit, photosynthetically active radiation, soil moisture, pre-dawn leaf water potential as an estimate of available soil moisture, leaf area index, wind speed (for eddy covariance measurements), and the interaction between air temperature and vapor pressure deficit. From these model fits could be discerned important asymptotes, transition points, and optima in the response of G_v to different drivers and to assess the significance of interactions among variables.

2.4 Results and Discussion

2.4.1 Meteorological trends

Trends in 2001 for mean daily air temperature, solar radiation, precipitation, vapor pressure deficit, and soil moisture are shown in Figure 2.12. The mean, minimum, and maximum air temperatures reached in 2001 were 16, -3, and 42 °C, respectively. Cumulative precipitation for the 2000-2001 rain year (approximately November 2000-October 2001) was only 340 mm (California Irrigation Management Information System, Station 131, Fair Oaks, Sacramento), an unusually dry year compared to the mean of 610 mm. No rain occurred in the fall of 2001, and winter rains did not begin until late January of 2001. For all of 2001, the total precipitation was 415 mm. Soil moisture exhibits a dramatic dry-down with the onset of summer.

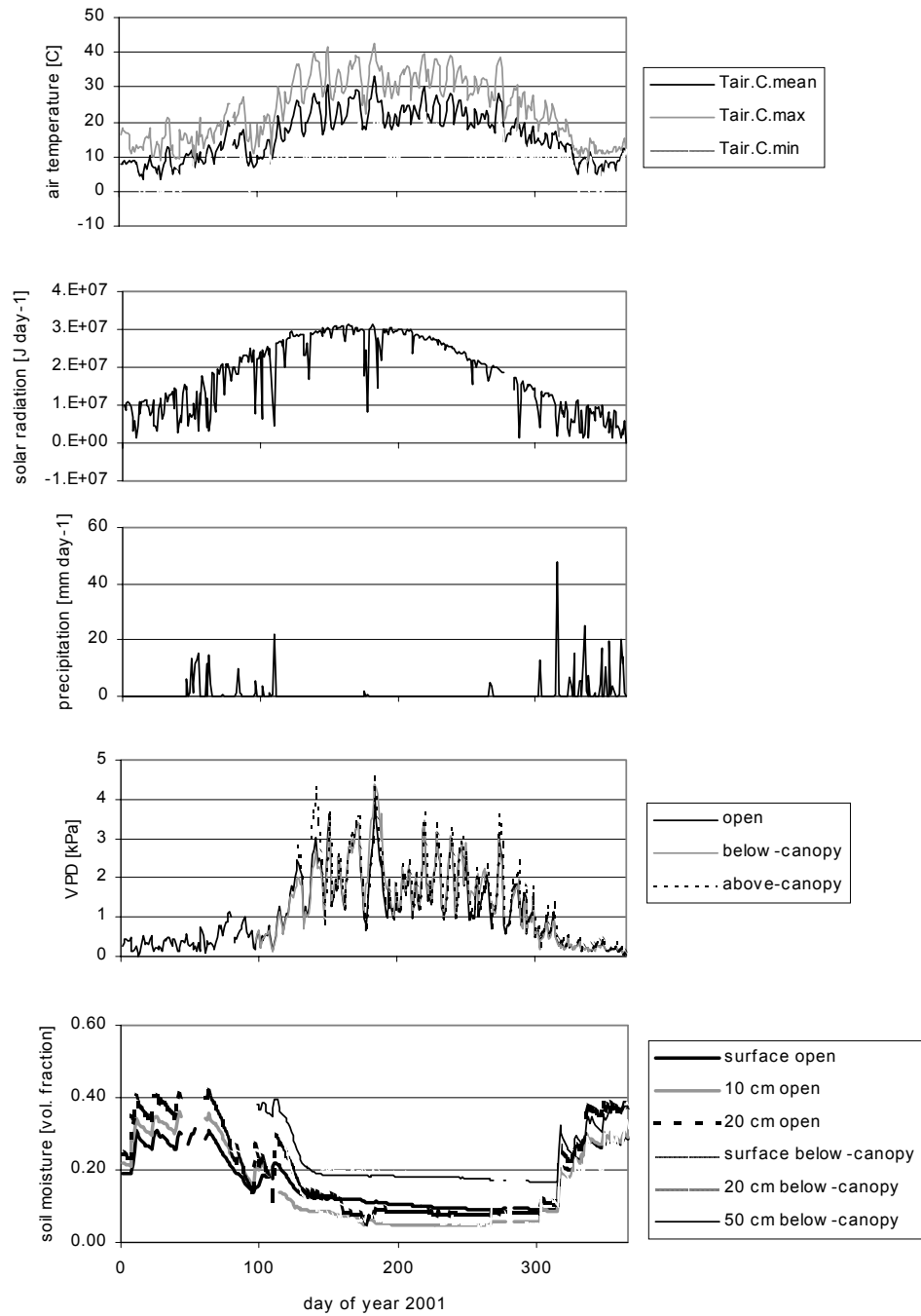


Figure 2.12: Daily values of air temperature, solar radiation, vapor pressure deficit, and soil moisture for 2001, Ione, CA, blue oak savanna and grassland sites.

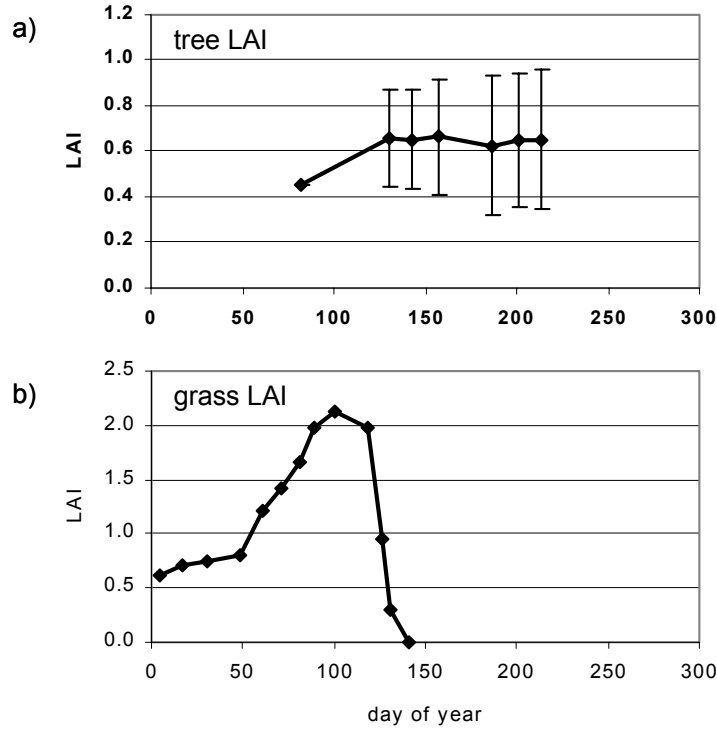


Figure 2.13: a) Tree canopy leaf area index as measured by the LAI-2000 (Li-Cor), with point-wise standard errors. Tree mean maximum LAI matches allometry estimates of 0.62 LAI. b) Grass LAI from Xu, et.al. (unpublished, mixture of harvests and estimates from fraction of absorbed photosynthetically active radiation; no standard errors available). Ione savanna, 2001.

2.4.2 Leaf area index

Leaf area index of the trees as estimated from LAI-2000 (Li-Cor) transect measurements is shown in Figure 2.13, together with leaf area of the grasses (as measured by harvesting by Xu, Kiang, and Baldocchi, unpublished). It can be seen that the trees reach their peak LAI just as the grasses senesce for the summer. The trees were leafless until late March ($\sim$ day 80), with an average branch area index of 0.45, then reached maximum leaf area within a month, about 0.65 at the 0.2 km scale (assuming branch area is not merely

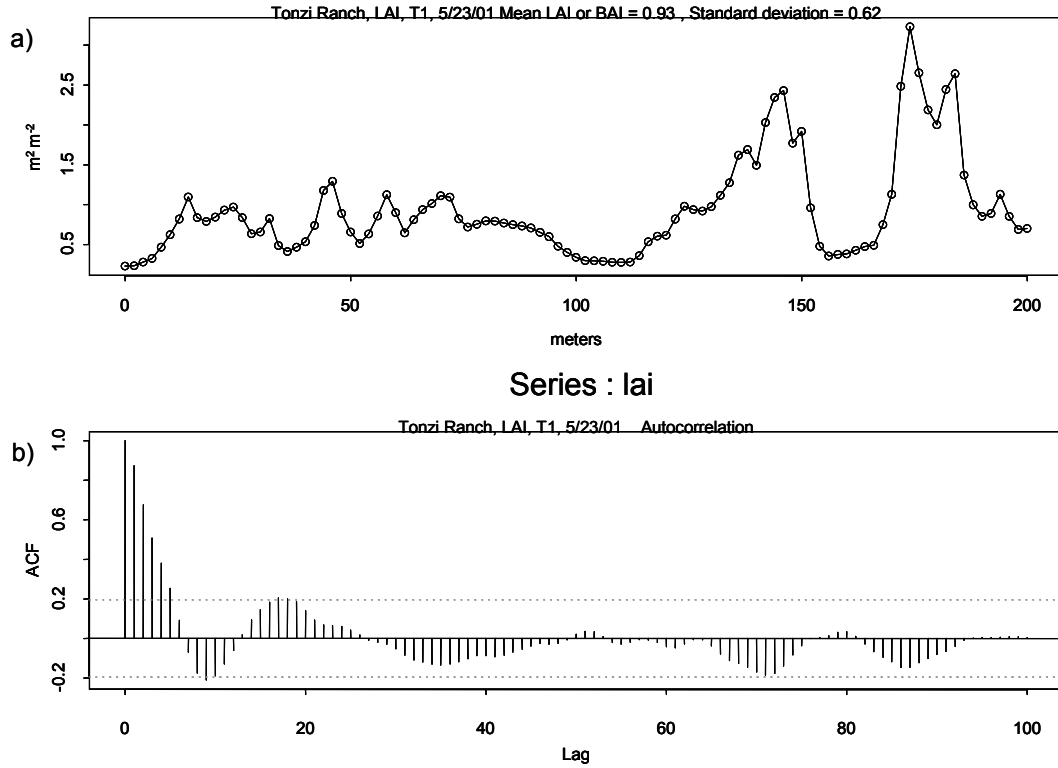


Figure 2.14: a) LAI along a 200 m transect in overstory eddy flux tower footprint. b) Autocorrelation function of LAI showing scales of tree clumping. Ione, CA, savanna site, May 23, 2001.

subtractive). However, spatial variation at this scale is fairly pronounced, with the three 200 m transects varying at peak LAI from a mean of only 0.34 (an area where trees had been cleared in the past) to 0.93 (along the main tower footprint). The pattern of LAI measured along the tower footprint transect is shown during peak LAI in May in Figure 2.14. The autocorrelation function plotted in the lower figure shows an underlying sinusoidal model in the horizontal canopy distribution of the trees, with highest autocorrelation (>0.6) below 3 m (the scale of a tree crown) and low positive autocorrelation (< 0.2) at around 20 m, giving the approximate scale of tree clumping. The clumped distribution of the trees violates the ideal assumptions (horizontal homogeneity) of the optical method of the LAI-2000, and

therefore these measurements are best used as a measure to monitor trends in LAI during the peak growth period. As the leaves senesced with summer drought, they still remained on the trees, and so the optical methods were not useful thereafter, since dead and green leaves on the branches could not be distinguished.

Litterfall measurements by Battles, et.al. (personal communication) yielded estimates of leaf biomass of 500 to 800 kg ha⁻¹ yr⁻¹, with the lower value derived from randomly placed baskets and the higher value derived from baskets placed under the trees and scaled by canopy cover. Leaf specific dry weight was 0.0136 ± 0.014 g cm⁻². Therefore, dividing total leaf biomass by leaf specific weight gives an LAI range of $0.37 - 0.59$ m² m⁻².

Karlik (2002) conducted whole-tree harvests of 14 blue oaks in 2000 at a Sierra Nevada foothills area approximately 280 km southeast of the Ione savanna site. The tree density of this sample was 2.3 times that of the tree density at the Ione savanna site, such that the total leaf area index of their site was 1.8 m²m⁻². Their leaf specific weight was also slightly higher at 0.0166 g cm⁻². If Karlik's allometric relations for tree leaf area vs. diameter at breast height are transferred to the Ione savanna site trees, the mean individual tree LAI at Ione is 1.6 m² m⁻² (leaf area per canopy projected area), such that, multiplying with the Ione canopy cover of .39 gives an estimate of a peak leaf area index of 0.62, which is the same as the averaged transect measurements with the Li-COR LAI-2000. Recall also that 2000 was a wet year, whereas 2001 was a very dry year, such that the LAI in 2001 is likely to correspond to the lower estimates.

In summary, the LAI estimates by optical, litterfall, and allometric estimates were 0.34-0.93 (mean 0.62), 0.37-0.59, and 0.62, respectively. As it is expected that the litter-

fall estimates to underestimate LAI, the means obtained from the optical and allometric methods, 0.62, are taken as the representative peak LAI for the Ione savanna site.

2.4.3 Tree leaf twig xylem water potential

The April-August 2001 trends in blue oak leaf twig xylem water potential are plotted together with maximum air temperature in Figure 2.15. Maximum daily air temperature and the difference between maximum and minimum air temperatures (circles) are also shown with the difference between pre-dawn and mid-day xylem water potentials (triangles). The twig xylem water potentials decline monotonically from pre-dawn levels of -3 bar to -45 bar. Meanwhile, the difference between pre-dawn and mid-day values correlates positively with the difference between maximum and minimum daily temperatures, which peak in June (day 158). Xylem water potentials were not measured after August, due to a dearth of green leaves available for sampling. Similarly, Griffin (1973), in a 3-year survey of blue oak water potentials at the Hastings Natural History Reservation (200 km south of Ione, along the coast) also found tensions reaching to an extreme of -42 bar in blue oak by the end of the growing season. From his observations, based on the pattern of pre-dawn xylem water potentials monotonically decreasing through the summer drought until senescence, Griffin concluded that blue oaks do not access deep water sources, but senesce in response to water deficit.

On day 158, daytime patterns in leaf twig water potential were measured on three of the sap flow trees, with results plotted with vapor pressure deficit in Figure 2.16. After reaching a mid-day extreme, leaf water potential recovers toward the late afternoon. These daytime trends correlate positively with vapor pressure deficit, with leaf twig water potential

Ione Savanna Leaf Water Potential: Site Means

Mid-day 116, Trees 245, 252, 255 only.

Mid-day 131, Trees 71, 72, 78 only.

Mid-day 187 and 201 are interpolated.

Not corrected for branch height.

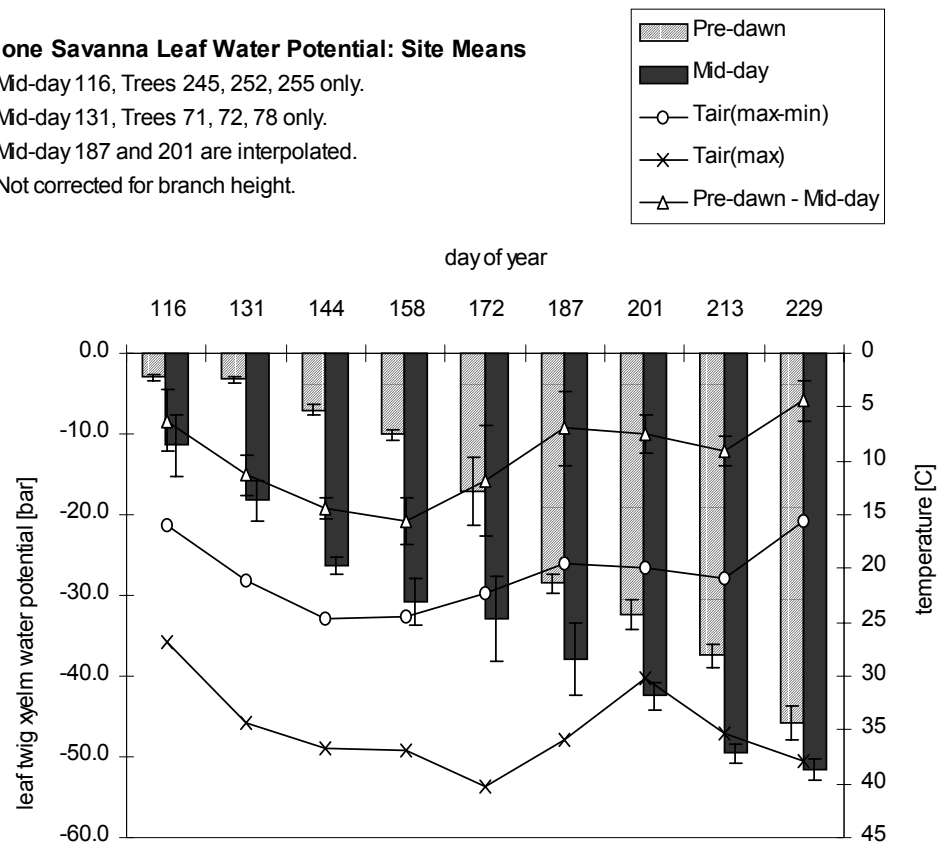


Figure 2.15: Leaf twig xylem water potential trends in *Q. douglasii*, Ione savanna, days of year 116-229, April 26-August 17, 2001.

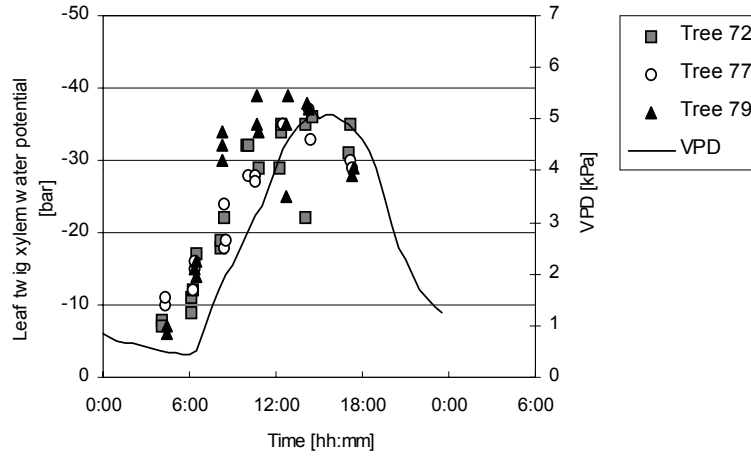


Figure 2.16: Daytime pattern in leaf twig xylem water potential in *Q. douglasii*, and vapor pressure deficit (VPD), Ione savanna, day of year 158, June 7, 2001.

trends lagging vapor pressure deficit by 2-3 hours.

2.4.4 Soil moisture

The soil moisture profiles calculated in terms of potential (bar) are shown with the leaf twig xylem water potentials in Figure 2.17a. The time course of the soil moisture profile is also given in volumetric fraction units in Figure 2.17b to make it easier for the reader to distinguish soil moisture at the 20 cm and 50 cm soil depths, since the hyperbolic relation between volumetric soil moisture and soil water potential (curve fit to the Ione savanna soil by Xu, unpublished) means that for moisture soil, water potential is closer to zero and changes very little for a change in soil moisture. In terms of potential (MPa), the 20 cm and 50 cm depths have very close, fairly wet values, while the surface soil layer reaches very negative potentials in the sensitive region of the soil moisture release curve. The wide vertical spread in the data for the surface layer is due to diurnal fluctuations. The

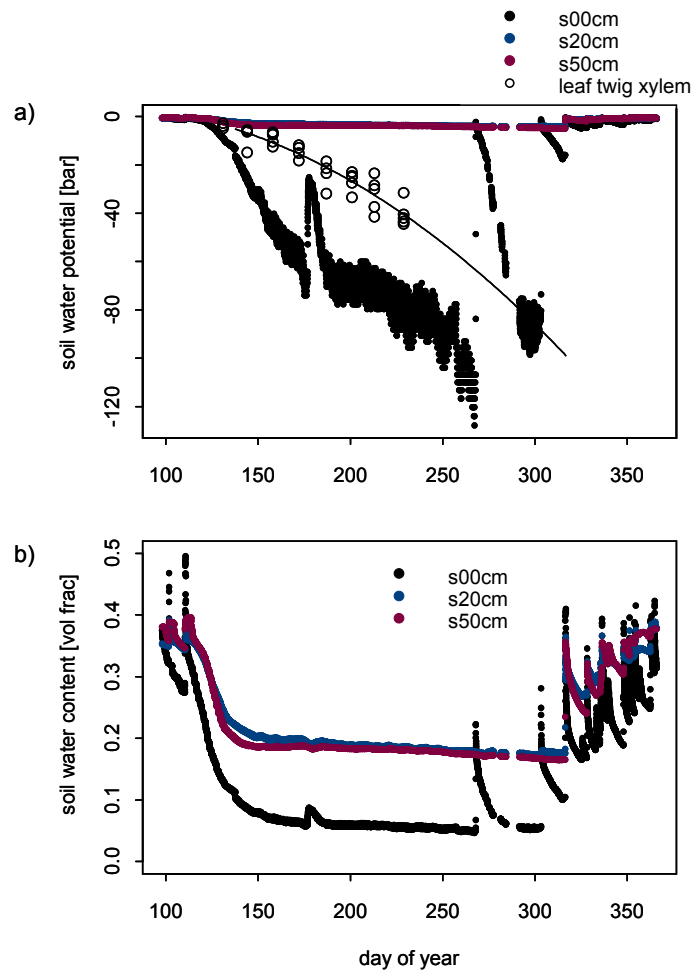


Figure 2.17: a) Soil water potential depth profile (MPa) with pre-dawn leaf water potential (open circles and fitted curve). b) Soil moisture profiles in units of volumetric fraction. Ione savanna site, 2001.

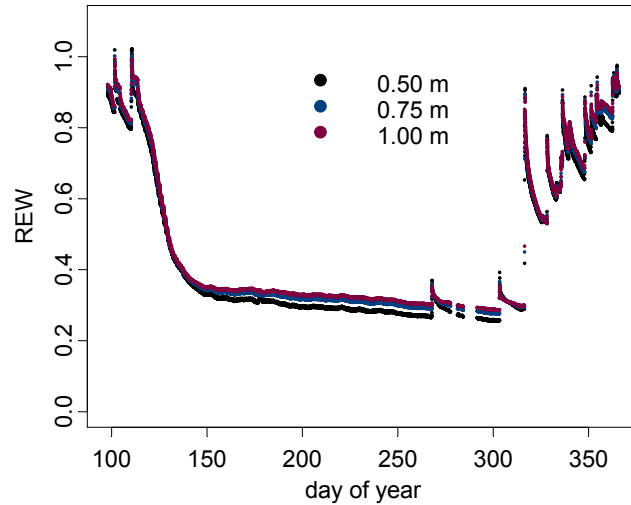


Figure 2.18: Soil relative extractable water content (REW) for different average soil depths. Ione savanna, 2001.

concurrent pre-dawn leaf twig water potential values indicate that the blue oaks' rooting depths are either primarily in the upper 20 cm or do not equilibrate to deeper soil moisture values.

Figure 2.18 shows estimates of relative extractable water for the Ione site in 2001, calculated from a depth-weighted average from the soil moisture sensors' vertical profile and for different possible soil depths at bedrock. Since the depth of the soil at the Ione savanna site varies between 0.5 m and 1.0 m, the REW may consequently vary locally. Figure 2.18 therefore shows what this range in variation could be, and provides some sense for the range of error in estimating a characteristic REW for the entire site. Since the absolute average soil depth for the entire site cannot be estimated without further soil profile measurements (forthcoming for this site), later analyses in this study rely on an

estimate of average soil depth as 0.6, which is the value for blue oak root depth found in an ecohydrological probabilistic analysis of soil moisture at the Ione savanna (Kiang, this dissertation).

2.4.5 Sap flow

To provide comparisons to other sap flow measurements in the literature, presented here are results for sap velocities (cm hr^{-1} and mm s^{-1}), tree volumetric sap flow rates by tree size ($\text{cm}^3 \text{ hr}^{-1}$ and kg hr^{-1}), sap flux density by tree size (sap flow volumetric rate, $\text{cm}^3 \text{ day}^{-1}$, per sapwood area, cm^2 , giving cm day^{-1}), and total stand transpiration (per ground area, mm day^{-1}).

Sap velocities and radial trends

The sap velocities for the individual trees at different depths into the sapwood are shown in Figure 2.19 for Julian days 114-120, a period approaching peak flow rates. The peak sap velocities of $30\text{-}50 \text{ cm hr}^{-1}$ in the outer sapwood position are comparable to those found for *Eucalyptus wandoo* (Farrington, et.al.,1994), for yellow poplar (Wullschleger and King, 2000), and for sessile oak (Granier, 1994). Velocities for sessile oak found by Raschi, et.al. (1995) were an order of magnitude lower, but their measurements covered only a few isolated days. Since most studies of radial trends are rarely long-term, most researchers do not necessarily cover periods of peak flow, such that comparisons of the magnitudes of sap velocities in different species are not possible or useful from the available data. The large vessels of ring-porous trees would be expected to have much high potential sap velocities than the sapwood of diffuse- or non-porous trees. The highest sap velocities found were for

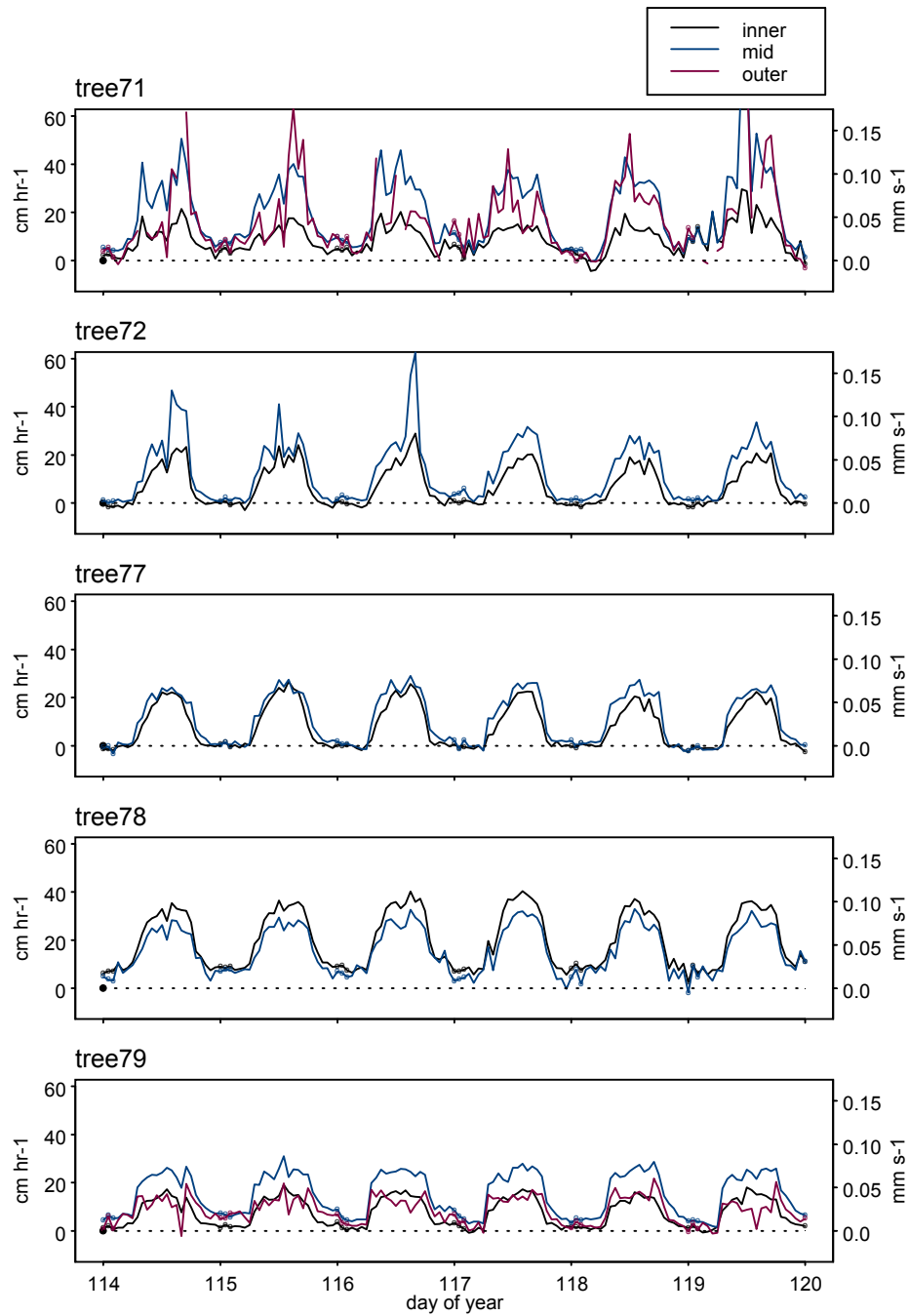


Figure 2.19: Radial patterns in sap velocity in blue oak (trees 71, 72, 77, 79) and grey pine (tree 78). Radial positions are: outer - at sapwood/bark boundary, mid - 1 cm depth, inner - 2 cm depth. Ione savanna site, 2001.

kiwifruit at 80 cm hr^{-1} (Edwards and Warwick, 1984).

The negative nighttime values for Tree 71 in Figure 2.19 could be due to actual negative fluxes at night, or simply due to greater sensor noise at low flows. Analysis of the full-year data in the next section will show whether this is a common behavior of this tree or merely noise. The positive non-zero values for the pine tree, Tree 78, are likely due to night transpiration, a phenomenon which has been observed for many species (Donovan, et.al., 2001).

There appear to be inconsistent radial trends in the blue oaks. Due to the noisiness of the outermost probe data, these data had to be discarded for two of the trees. The loss of the outer ring data could lead to either over- or under-estimation of sap flow for those trees, if the interpolation technique used did not sufficiently approximate the outer ring sap velocity, but there is not sufficient information for error propagation here. In the spring, when the rapid sap flow is transported by the largest outer xylem vessels, loss of the outer ring data would lead to underestimation of sap flow. Overestimation could occur in the summer if extrapolation of the inner ring sap velocities is done when the outer vessels have cavitated and are not conducting. Tree 71 shows the outermost sap velocity to be approximately the same as the next deepest probe at 1 cm, whereas Tree 79 exhibits a curved distribution, with sap velocity peaking in the middle probe. Several researchers have observed that the sap velocity may have increasing or decreasing radial trends into the sapwood for many species (see extensive table of comparisons of different studies by Phillips, et.al., 1996). Given the ring-porous anatomy of oaks and the tendency of older vessels to fill up with tyloses following embolisms, it would be expected that the inner sapwood would

be less conductive. Studies of ring-porous trees by Miller, et.al. (1980), Ellmore and Ewers (1986), Cermak, et.al. (1992), Granier, et.al. (1994), Raschi, et.al. (1995), and Tognetti, et.al. (1996) all show sharp decreases in sap velocity (sap flux density, in the case of Granier-type probes) deeper into the sapwood, implying that the bulk of the conductance is through the most recent annual ring; only a study by Phillips, et.al. (1996) on *Quercus alba* shows no consistent radial trend. The computer tomography work of Raschi, et.al. (1995) and Tognetti, et.al. (1996) showed a great deal of circumferential variation in sap velocities. Meanwhile, since only the largest vessels tend to embolize, the radial trend may be seasonal, with faster transport through new, large vessels in the wet spring, then maintenance of low transport rates in inner vessels carrying the bulk of the sap during dry periods of lower water potential.

The pine tree, tree 78, also exhibits some radial variation. As the outermost ring is subject to the most noise, because it was difficult to discern the exact sapwood/bark boundary for sensor placement, some outer ring data had to be discarded and values approximated by projecting the trends from the inner rings, which exhibited clear trends. The greater potential velocities of the outermost ring are apparent in the largest blue oak, Tree 71, despite noisiness of the data. Mean maximum sap velocities achieved by these oaks in mid-spring were around 40 cm hr⁻¹, with the highest around 50 cm hr⁻¹ for the outer ring of the largest blue oak, Tree 71 (42.5 cm dbh).

Tree sap flux densities and sap flow rates

Sap flux densities (cm³-H₂O hr⁻¹ cm⁻² sapwood area = cm hr⁻¹) and volumetric sap flow rates (1000 cm³ hr⁻¹ per tree) for the individual trees are shown in Figure 2.20,

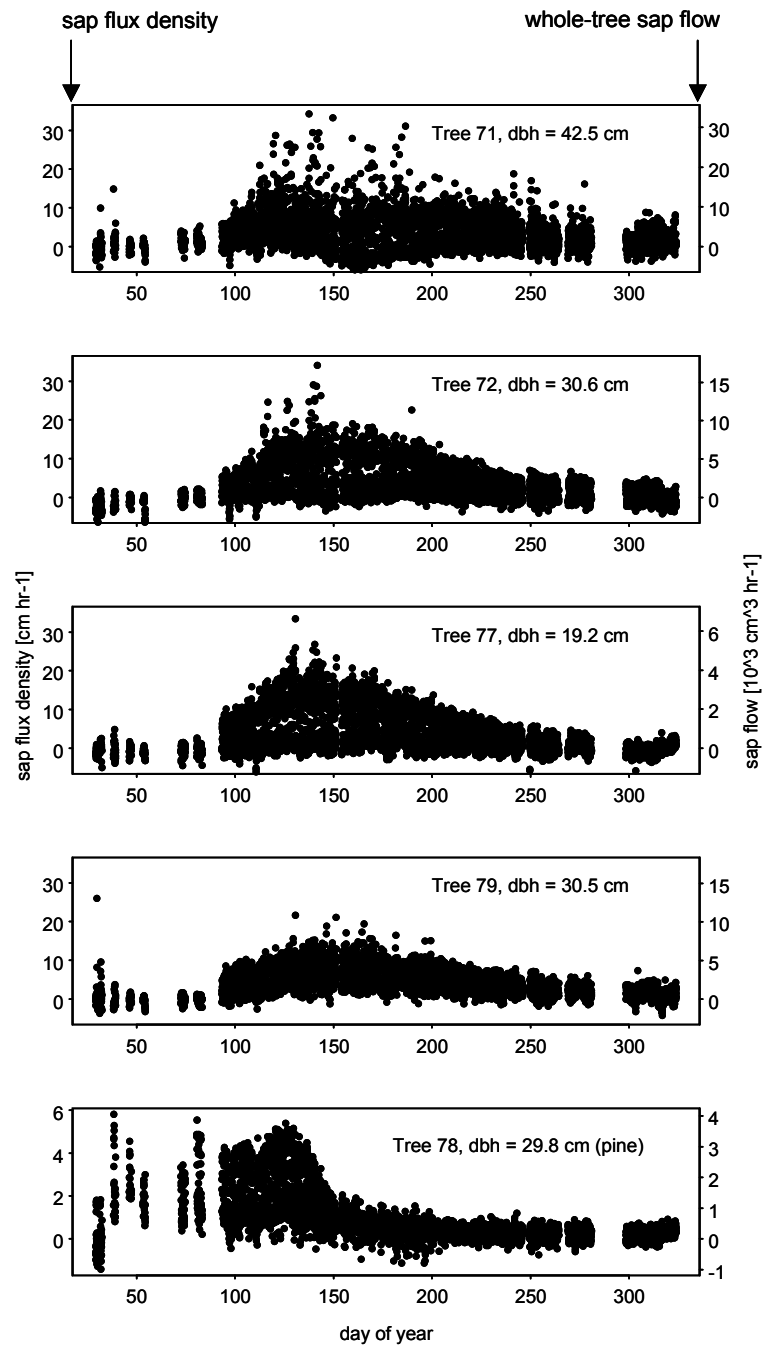


Figure 2.20: Sap flux densities per tree sapwood area (left axis) and whole-tree sap flow rates (right axis, sap flux density $\times$ tree sapwood area) for blue oaks (Trees 71, 72, 77, 79) and grey pine (Tree 78). Blank areas are periods of missing data. Ione savanna, 2001.

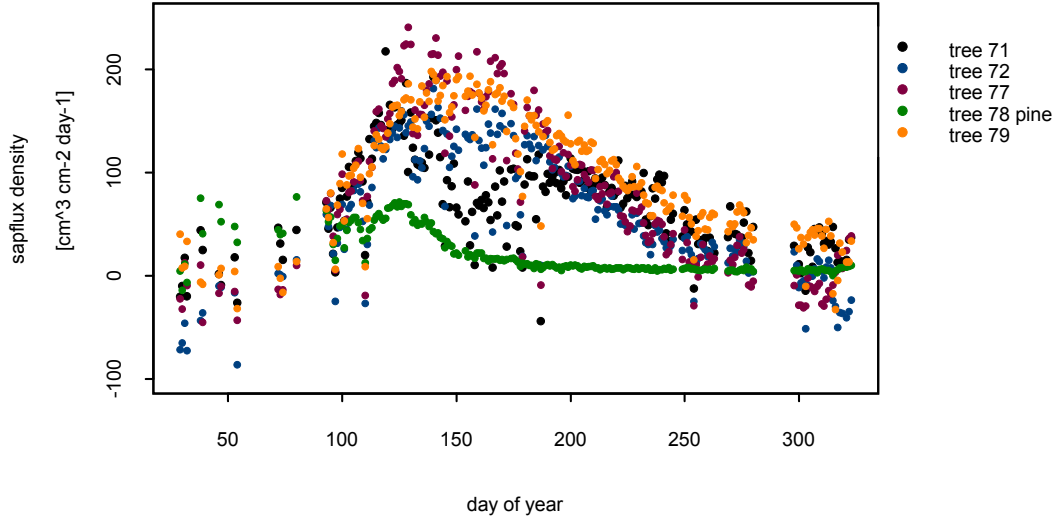


Figure 2.21: Daily total sapflux density of individual trees, in sapflow volume rate per sapwood area ($\text{cm}^3 \text{ day}^{-1} \text{ cm}^{-2}$), Ione savanna, 2001.

with sap flux density on the left axis and volumetric sap flow on the right axis (note that the scales for the sap flux density left axis are all the same for the blue oaks, but different for the pine tree in the bottom graph). While the volumetric sap flow rate increases with tree size, as expected, the per sapwood area sap flux density appears independent of tree size on a daily basis. Overlaying their daily total sap flux densities (Figure 2.21) shows that on a daily basis, all size classes of the blue oak trees exhibit about the same overall flux densities. The largest tree, Tree 71, exhibits a clear trend of negative sap flow at nighttime during the peak spring growth period, such that its total daily sap flux density is reduced below that of the other trees, but then recovers again to match during the summer. It is unclear why the largest tree exhibits negative sap flow. In roots, negative flow is a manifestation of hydraulic lift (Burgess, et.al., 1998), but its occurrence in the stem a blue oak requires further explanation. In sharp contrast, the pine tree, Tree 78, has dramatically lower sap

flux densities than the oaks, about 4 times lower in peak magnitude. However, during the winter months before the blue oaks leaf out (mid-March), the evergreen grey pine maintains close to its peak sap flux density while the oaks are dormant.

The non-zero (both negative and positive) blue oak sap fluxes during winter indicate that the oak boles may still be conductive of water, though not for leaf transpiration. Why they should be conducting during the winter may perhaps be only a phenomenon of the wood response to environmental conditions, but more likely very low flow values are causing noise in the data. The maximum sap velocities of the blue oaks average about 20 cm hr^{-1} during the peak season, sometimes reaching as high as 30 cm hr^{-1} , while the pine's maximum is about 5.5 cm hr^{-1} . On a daily basis, during the peak season, the oaks' sap flux density is as high as 200 cm d^{-1} , while the pine only reaches 77 cm d^{-1} . For comparison, other researchers have measured peak hourly sap flux densities as given in Table 2.6. Needleleaf trees consistently have lower sap flux density than hardwoods. Pines have a non-porous wood anatomy, which is necessarily less conductive than the ring-porous anatomy of the oaks, which is adapted to have large vessels for rapid transport of water during the wet, peak growing season, and smaller vessels during the summer to maintain capillary flow during times of low water potential. (Note that some researchers calculate sap flux densities on a per-crown area basis, rather than on a per-sapwood area basis, making some intercomparisons difficult. E.g. Kelliher, et.al., 1992; Arneeth, et.al., 1996; Wullschlegel, et.al., 2000). *A. saccharum*'s sap flux density in the table is calculated from radial profiles of sap velocity in Pausch, et.al. (2000).

The blue oaks exhibit a remarkably steady linear decline in maximum sap flow

Species	Maximum sap flux density per sapwood area (cm hr ⁻¹)	Source
<i>Taxodium distichum</i>	4-7	Oren, et.al., 1999
<i>Pinus cembra</i>	5	Anfodillo, et.al., 1998
<i>Pinus sylvestris</i>	7.5	Granier, et.al., 1996
<i>Pinus taeda</i>	7-11	Oren, et.al., 1998
<i>Acer saccharum</i>	7.6	Pausch, et.al., 2000
<i>Pseudotsuga menziesii</i>	12	Granier, 1987
<i>Picea abies</i>	15-20	Köstner, et.al., 1998
<i>Larix decidua</i>	25	Anfodillo, et.al., 1998
<i>Quercus petraea</i>	25	Granier, et.al., 1996
<i>Eucalyptus salmonophloia</i>	34	Farrington, et.al., 1994
<i>Populus tremuloides</i>	30-40	Hogg, et.al., 1997

Table 2.6: Maximum sap flux densities for various species, based on sapwood area.

rates over the course of the summer, in stark contrast to the pine tree, Tree 78, which exhibits sap flow during the winter months when the oaks are still leafless, and then reduces sap flow sharply in May at the same exponential rate as soil moisture dry-down. This markedly linear trend in the oaks, in spite of the exponential soil moisture decrease, must be a manifestation of drought tolerance abilities of the blue oaks, such as alteration of their osmotic potential to counteract the effects of extremely low soil water potentials (Momen, et.al., 1994), utilization of stored water, and, speculatively, stomatal closure to guard against cavitation. The linear trend is reproduced by eddy flux measurements, as will be shown later. The largest blue oak, Tree 71, exhibits the least decline with summer drought, and appears to exhibit a period of regular reverse sap flow at nighttime during June, unlike the other trees. This behavior in fact only occurs in the innermost ring of Tree 71, and may be an unexplained radial sap transport phenomenon or a figment of changing inner sapwood moisture content during the spring. Of the two mid-size oaks, Tree 72 (dbh 30.6 cm) exhibits consistently greater maximum sap flow rates and sap flux densities on an

hourly basis than Tree 79 (30.5 cm dbh), despite their similar sizes; however, at a daily scale there is not a significant difference, or Tree 79's daily total may be slightly greater. The differences between Trees 72 and 79 are not likely due to canopy position, since both are the same size and occur at about the same spacing from other trees; other possible explanations for their differences could be circumferential variation, life history (e.g. disease or damage), or microsite variation, such as in soil depth and root access to moisture.

Since all of the blue oaks' sap flow densities are similar, this accordance with pipe model theory (Shinozaki, et.al., 1964) indicates that sap flow may not necessarily have to be partitioned by tree size or canopy status when devising an expedient sap flow monitoring program for an open-canopy oak savanna, but sap flux density may be easily extrapolated over the stand sapwood area. Other researchers have found that vertical canopy stratification results in different microclimates for dominant and sub-canopy trees, such that the observed sap flux density per sapwood area is not consistent per tree (Wullschleger, et.al., 2000; Köstner, et.al., 1992). The openness of a savanna may make the canopy structure effect negligible for estimating stand transpiration for trees like the blue oaks. On the other hand, tree size may differentiate trees by their access to soil moisture. Griffin (1973) found a difference in water status of different age/size classes of blue oaks, with saplings and seedlings reaching to lower leaf twig water potentials than mature trees; however, since mature trees are the main contributors to stand transpiration, while small trees contribute little sapwood area, and extremely large trees are rare and contribute only a small percent of total fluxes, the distinction between the smallest and largest trees may compensate each other for the purposes of calculating transpiration.

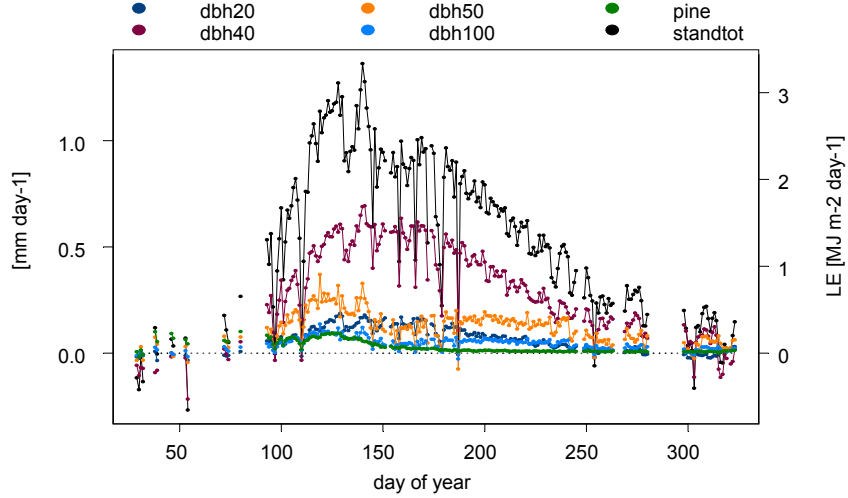


Figure 2.22: Stand transpiration, daily total and breakdown by blue oak dbh class and pine. Dbh values are in cm, giving upper value category range. Ione, California, savanna site, 2001.

2.4.6 Stand transpiration, sap flow and eddy flux

Figure 2.22 shows daily totals of sap flow scaled to the stand level, with breakdowns by blue oak dbh class and pines (dbh value in cm is the upper value of the dbh category). Since the sap flux densities are the same across size classes of oaks, the share of a size class in total transpiration directly corresponds to its share of total stand sapwood area. The pines, in green, contribute the least to total transpiration, but during the winter months when the oaks are leafless, the pines contribute all of the tree transpiration.

Figure 2.23 shows transpiration as estimated by sap flow, compared to latent energy fluxes as measured by eddy covariance (open grassland ("open"), under tree canopy ("understory"), and above the whole savanna system ("overstory"). The figure shows the daily sums (summing method described in Methods) of half-hourly fluxes of three eddy

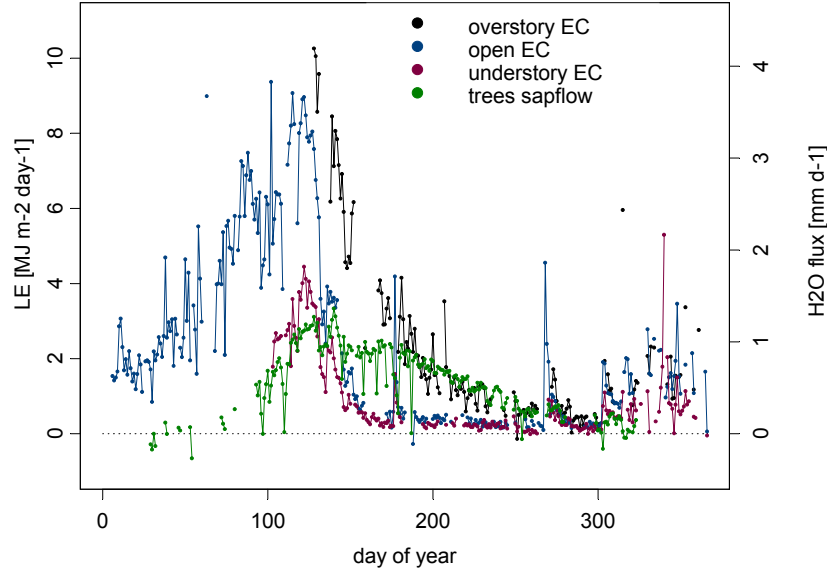


Figure 2.23: Daily sum of latent energy fluxes [MJ day^{-1}] and tree transpiration from overstory, understory, and open grassland eddy covariance measurements, and from sapflow measurements. Ione savanna, 2001.

covariance stations and hourly sap flow. The open grassland areas show considerably higher fluxes in the winter-spring (Days 0-120) than the understory herb layer, since the open areas are not shaded by the trees. The trees account for all the evapotranspiration after the understory has senesced by the beginning of June (Day 152), while there remains some soil evaporation in the understory; the understory evapotranspiration then recovers with the fall rains (around Day 180).

How well the sap flow measurements capture the daily sums of tree transpiration can be checked against the eddy covariance measurements. Figure 2.24 shows whole-savanna evapotranspiration as estimated by the overstory eddy flux in comparison to the sum of the below-tree eddy flux and sap flow measurements. The understory and open

grassland eddy fluxes were each scaled by canopy cover fraction and 1 minus canopy cover fraction, respectively, in a patch-type scaling. The summed estimate of above-tree fluxes slightly underestimates total fluxes during the peak spring period, but then matches well with the overstory tower measurements during the summer. Doing differencing between the overstory and below-tree eddy covariance measurements will help better to discern where the sap flow and eddy covariance techniques differ. Figure 2.25 shows sap flow estimates of tree transpiration compared to estimates from taking the difference between the overstory and below-tree eddy covariance measurements (the overstory measurements are included as a visual reference for magnitudes). Both sap flow and eddy covariance estimates match well in the summer when the understory is dead and the trees account for all transpiration. However, in the spring, eddy covariance estimates of peak flows are much higher. As has been observed in other cases of comparing eddy fluxes to sap flow measurements, eddy flux measurements are always larger in peak times than sap flow. The eddy covariance peak estimate of tree transpiration is 2.2 mm d^{-1} , compared to the sap flow peak of 1.4 mm d^{-1} during the early spring, but then the values converge with the onset of the dry summer. Eddy covariance estimates continue to coincide with sap flow with the arrival of early winter rains. The difference in magnitudes during the wet or humid seasons is consistent with observations of other researchers (Arneeth, et.al, 1996; Wilson, 2001) who also compared eddy covariance and sap flow. Some possible explanations for this underestimation by sap flow or overestimation by eddy covariance are: 1) much of the most rapid flow through the outermost, large xylem vessels during the spring is missed by the heat pulse velocity sensors; 2) the capacitance of the trees is not accounted for by sap flow measurement techniques, as

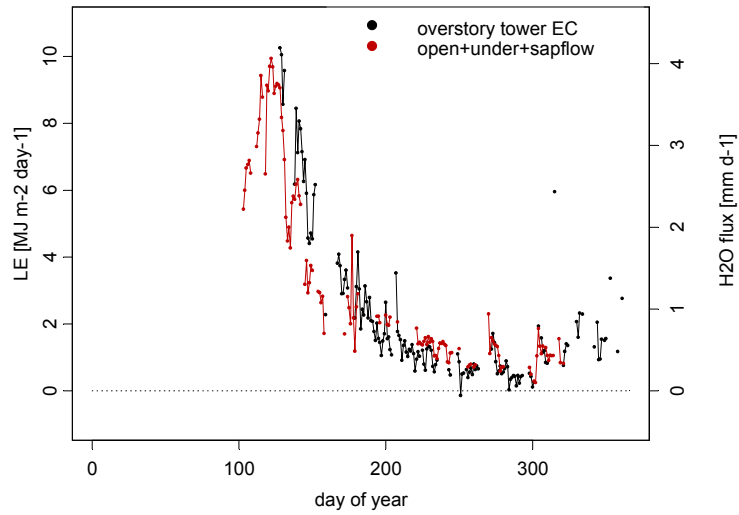


Figure 2.24: Whole-savanna evapotranspiration as estimated by the overstory eddy flux measurements and by summing sap flow and below-tree eddy flux. Ione savanna, 2001.

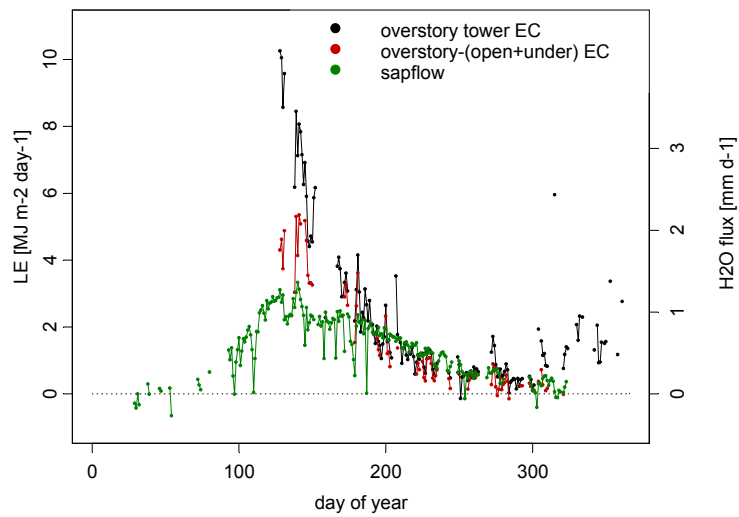


Figure 2.25: Tree transpiration as estimated by the sap flow measurements, and by difference between overstory and below-tree eddy flux towers. Overstory eddy flux measurements are included as a reference for magnitude of fluxes. Ione savanna, 2001.

shrinkage of the bole with loss of stored water is not quantified; 3) dew evaporation during humid periods could possibly be significant (Monteith, et.al., 1958; Garratt, et.al., 1988); 4) change in wood moisture content from the spring through the summer alters the thermal diffusivity of the wood leading to errors in the sap flow calculation.

Explanation 1, that the flow through the outermost xylem vessels is missed, is highly plausible, since the largest vessels were nearly the same order of magnitude (0.43 diameter) as the needle probe (1.275 mm) and could be most easily susceptible to disruption by the probes. As the spring sapwood would have grown over the sensors (installed in the winter), the lack of capture of the peak flows is most likely either due to the correspondence between sensor scale and large vessel diameters (i.e. the sapwood cannot be considered homogeneous by the sensor in the vicinity of large vessels), or perhaps because new growth avoids growth of large vessels when an obstruction is sensed by the tree (speculation). This lack of capture of peak flows by sap flow sensors has been observed by other researchers on ring-porous species, also (Russell Scott, personal communication). Also, the outermost HPV sensors were subject to the most environmental noise and some of these data had to be discarded and estimated through extrapolation, the potential errors of which were discussed earlier. The blue oak radial profiles were also not nearly so dramatically changing, in contrast to that found by Granier, et.al. (1994) for *Quercus petraea*. It is known that ring-porous species rely on larger-size xylem vessels for rapid water transport during the peak growing season, and other researchers have found evidence that the smaller, inner vessels then account for more sap transport during the dry summer, since they can maintain capillary flow under very low water potentials when the larger vessels may cavitate (Phillips,

et.al., 1996). This pattern matches the Ione observations, since there is underestimation of sap flow during the spring when the outermost, large vessels could have been missed, whereas the summer sap flow and eddy covariance estimates of tree transpiration exactly coincide, when the outermost vessels were likely less responsible for most of the sap transport.

Bole shrinkage is also a possible concurrent explanation, since bole shrinkage does occur. Continuous dendrometer data was not available during the measurement period to monitor the rate of bole shrinkage, but these data would have to support shrinkage occurring during the period of rapid soil dry-down. Given the Ione site's open canopy and relatively arid system, the dew effect is most likely negligible. With the arrival of the first fall rains on Day 269, the difference between the overstory and understory eddy covariance estimates of tree transpiration continue to match with sap flow measurements, indicating that dew effects are not significant. Finally, wood moisture-dependent thermal diffusivity cannot be responsible for errors in estimated sap flow in the spring, because a higher wood moisture content at this time would imply a lower thermal diffusivity than the summer, whereas a higher value would be needed to produce a higher estimate of spring sap flow. Overall, the evidence seems to support errors in sap flow estimates from vessel damages as the most likely, such that eddy covariance data may be more reliable estimates of tree transpiration year-round for this open canopy system. Meanwhile, the fact that both measurements coincide during the dry summer encourages confidence in an absolute estimation of tree transpiration during that period.

2.4.7 Tree hydraulic conductivity

Tree hydraulic conductivity calculated from pre-dawn and mid-day leaf twig water potentials and sap flow are shown in Figure 2.26.

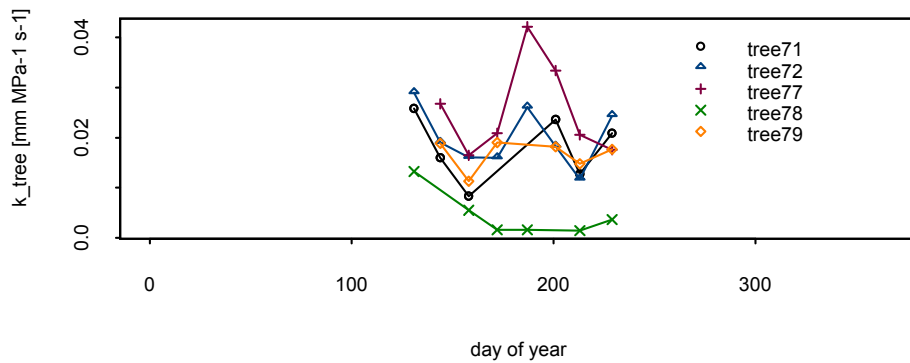


Figure 2.26: Tree hydraulic conductivity calculated from leaf water potentials and sapflow. Trees 71, 72, 77, 79 are blue oak (*Q. douglasii*), and Tree 78 is grey pine (*P. sabiniana*).

Among the oaks, there is not a monotonic trend in hydraulic conductivity, whereas with the pine there is a steady, emphatic decline. The hydraulic conductivity during the summer dry-down of the oaks is clearly not dependent on soil moisture. In the oaks, there is a consistent pattern of decline in the hydraulic conductivity from day 131 to 144 (mid-May) then a local peak between days 185 and 205 (July), and then a slight rise again on day 229 (mid-August). The pattern is most pronounced in tree 77, the smallest blue oak (dbh 19.2 cm). The pattern corresponds roughly to trends in the vapor pressure deficit, which implies that tree hydraulic conductivity calculated in this manner from sap flow and leaf

twig water potentials may not be the best indicator, since stomatal control rather than stem anatomy is limiting conductance; the same trend remains whether selecting for maximum or mean flux rates during the morning period. Nonetheless, these results show that the hydraulic conductivity of the blue oaks is not correlated with soil moisture, whereas that of the pines is. As mentioned before, blue oaks are able to alter their osmotic potential to maintain water potentials, an ability which may explain the difference seen here between the oaks and pine.

Although the tree hydraulic conductivity, as discussed earlier, is only a very rough indicator of tree physiology, the trends here imply a strong drought tolerance and maintenance of transpiration by the oaks, in contrast to the summer shutdown in the pines.

2.4.8 Tree canopy conductance

In this section are presented the temporal courses of tree canopy conductance and some traditional plots of the conductance versus well-known meteorological drivers, setting the stage for more rigorous, multivariate statistical analysis of the tree canopy conductance.

Tree canopy conductances, G_v , by inverting the Penman-Monteith equation for the morning hours of 9:00-12:00 are shown in Figure 2.27. Figure 2.27a shows the morning conductances as derived from eddy covariance data, and Figure 2.27b) shows that derived from sap flow data. Vapor pressure deficit is included in Figure 2.27c, as one major driving variable influencing canopy conductance which is inversely related to the conductance. The smoothed lines are fit by local regression (Venables and Ripley, 1994, S-Plus software), which fits a quadratic, weighting local points as more influential, not dissimilar to a moving average. The span of smoothing was simply chosen to provide a visual estimate of the

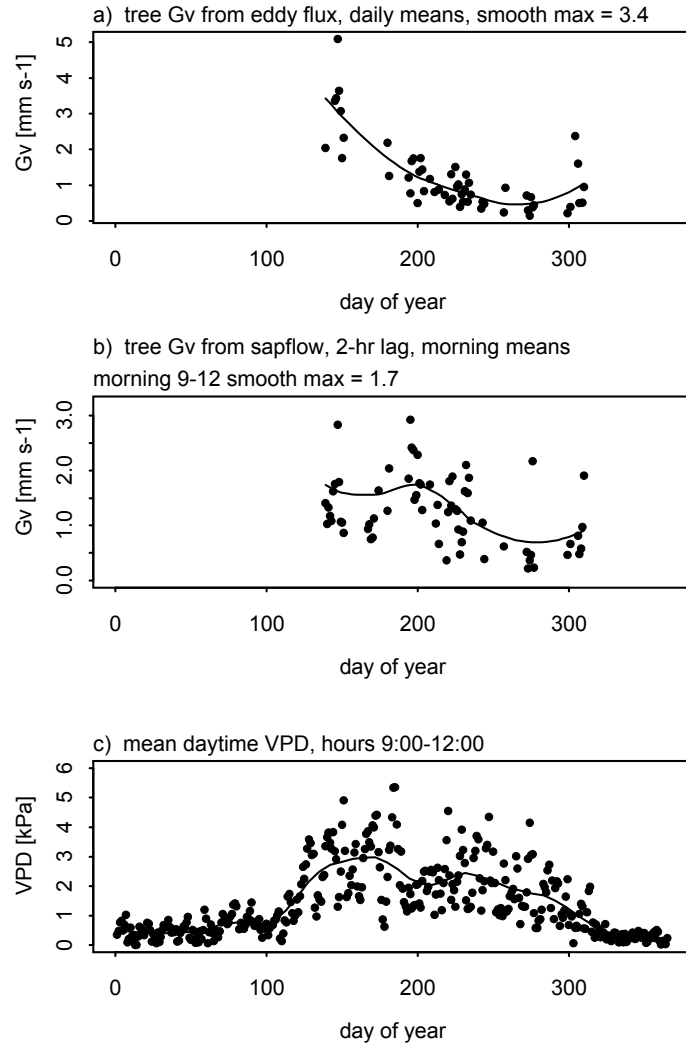


Figure 2.27: Daily means of tree canopy conductance, G_V , from inverting the Penman-Monteith equation using data from a) eddy flux, and b) morning sapflow with a 2-hour lag behind meteorological variables. Shown with c) mean daytime vapor pressure deficit. Ione savanna, 2001.

significant trends in the data. The daily mean G_v is greater in the spring for the eddy covariance fluxes than for the sap flow, consistent with the comments above about the latent energy fluxes during the wet versus dry seasons. Clearly, there is a decline in tree canopy conductance over the course of the summer. The greater variability in sap flow conductance may reflect merely the choice of smoothing span, or it may show how conductance is related to the inverse pattern of vapor pressure deficit prior to mid-August ($\sim$ day 230), but then remains low during soil moisture deficit and through the course of senescence.

The daily maximum values of canopy conductance are shown in Figure 2.28. Numbers shown include the mean of all the observed values (mean daily maximum), the maximum predicted from the smoothed curve fit, and the maximum of the observations. These daily maxima exhibit the same trends as the daily means, but with more noise as expected, since these are peak points during the day. The values are very low compared to the maximum bulk surface conductances for several vegetation types compiled by Kelliher, et.al. (1995), but which were for well-watered conditions and do not include semi-arid types. As the understory was separated from the tree fluxes here, the surface conductances and tree conductances are not strictly comparable, but, for reference, the Ione maximum canopy conductances (7.1 mm s⁻¹ for eddy covariance, 5.1 mm s⁻¹ for sap flow) are less than half that for well-watered temperate grassland and Eucalypt forest, which are in the low range of conductances.

Figure 2.29 shows the hysteresis commonly observed for the diurnal relation between transpiration, canopy stomatal conductance, G_V , and vapor pressure deficit, VPD. Here, the patterns of all days are color-coded by month and overlaid on the same plot,

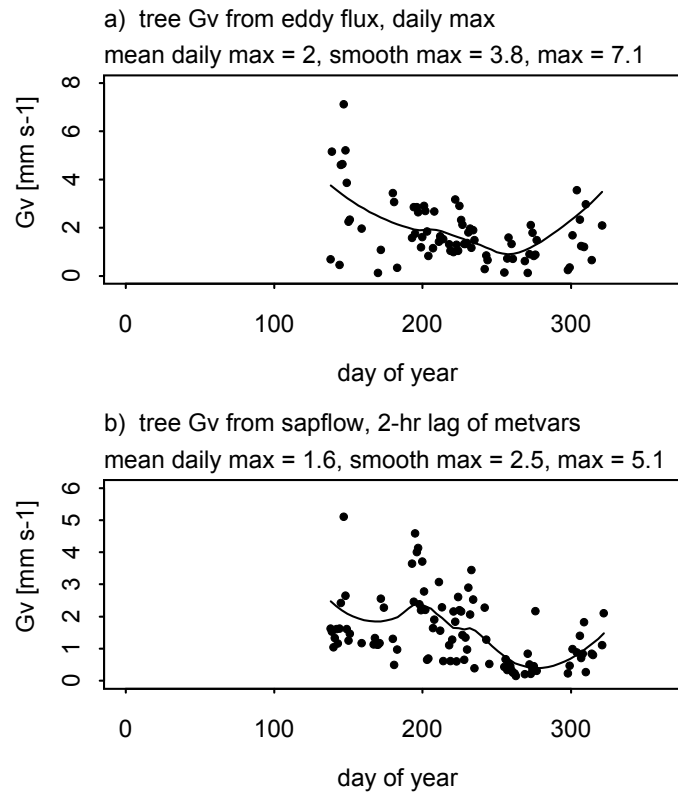


Figure 2.28: Daily maximum values of tree canopy conductance, G_v , from inverting the Penman-Monteith equation. Values shown are morning (9:00-12:00) averages for a) eddy flux, and b) sapflow with a 2-hour lag behind meteorological variables. Values given are the mean of the observations, the maximum predicted from the smoothed curve, and the maximum of the observations. Ione savanna, 2001.

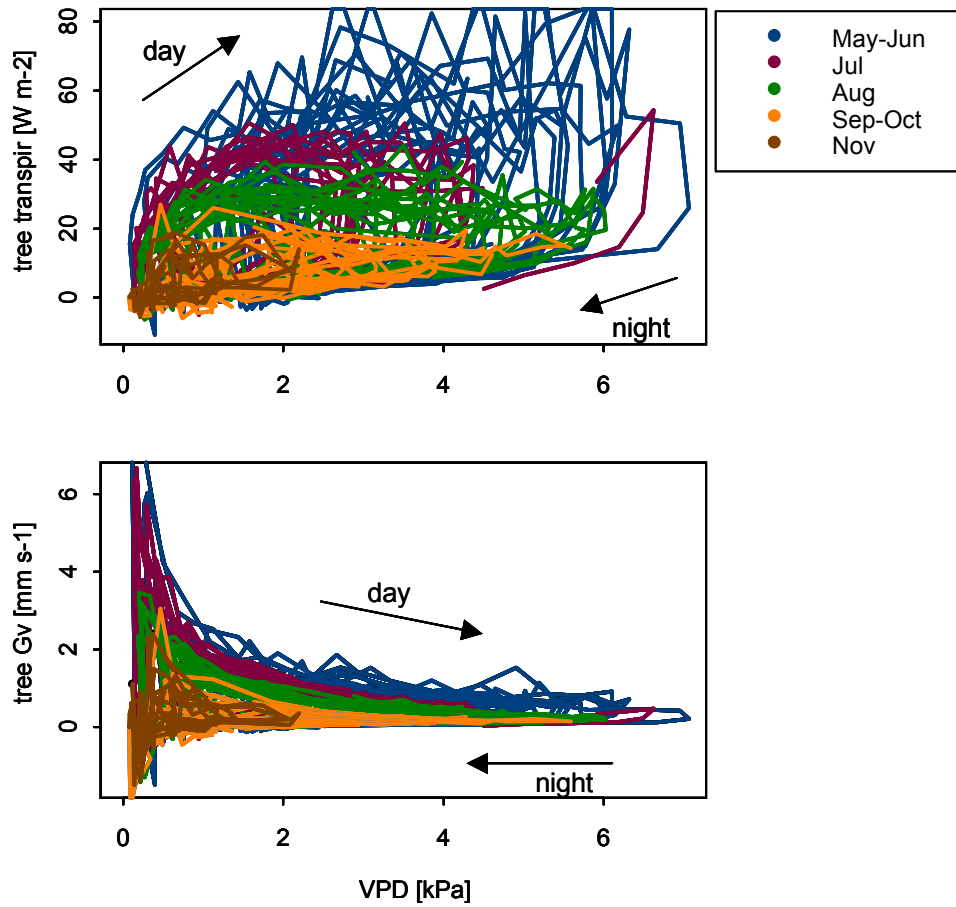


Figure 2.29: Diurnal hysteresis of tree canopy latent energy flux from sap flow (top figure) and conductance (bottom figure) with respect to vapor pressure deficit. Days are grouped by color by month. Arrows indicate direction of the diurnal cycles.

showing both the hysteresis with respect to VPD as well as the gradual seasonal trend of declining fluxes and conductances during the summer. The diurnal cycles follow the lines clockwise for each loop, with the upper half of each loop corresponding to the daytime, and the bottom half corresponding to nighttime. That the conductance decreases exponentially during the day while transpiration remains fairly constant indicates that stomatal control is being exerted to maintain steady transpiration as the daily VPD falls. The phenomenon is illustrative of the fact that canopy stomatal conductance is inversely related to VPD, but VPD is not the only explanatory variable. For example, low light in the evening decorrelates G_V and VPD, as the lower part of each curve corresponds to nighttime behavior. The marked seasonal trend emphasizes other factors, such as soil moisture, probably being important. Meanwhile, the fact that, for each cycle, somehow transpiration is maintained constant during the day despite changing VPD, leads to the question of what the mechanism is for such stomatal control: is it due to changing xylem water potential during the day (hydraulic conductance limitation a possible explanation), or cellular-level sensing of transpiration rate (as hypothesized by Mott and Parkhurst, 1991), or co-limitation with photosynthetic capacity, or other possibilities? The trends in these hysteresis curves motivate further types of analysis. (Note: the one diurnal cycle in July that extends out into the range for May-June is close to the June/July cut-off in the binning of the data, hence its departure from the bulk of the July cycles).

A traditional stratification of the light response of G_V (partitioning the data by VPD classes), is shown in Figure 2.30. One can see that both drivers, VPD and PAR, create distinct trends, but that other factors must also be causing the wide variation in G_V

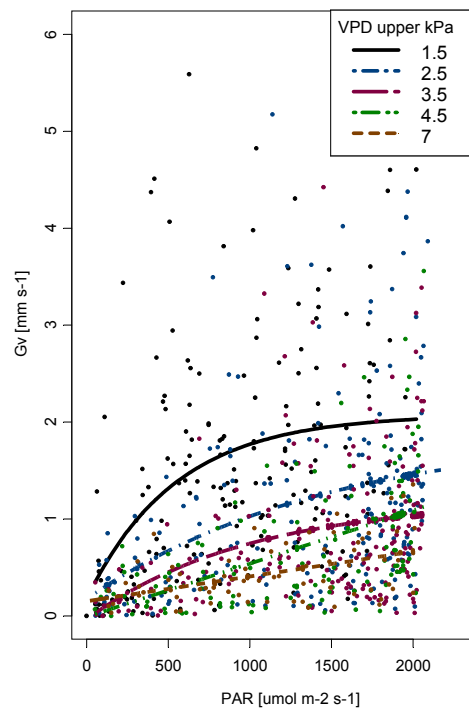


Figure 2.30: Light response of canopy conductance, G_v , stratified by VPD. Ione savanna, 2001.

about this response curves. These curves were generated by simple non-linear regression of a curve of the form $b3 - b2 * \exp(-b1 * PAR)$. For the upper two levels of VPD, a simple line fit was done, because the data could not converge to a curve of the exponential form, so the line fit shows the general trend and magnitude in the PAR response with increasing VPD.

Clearly, these traditional data plots show expected patterns. However, derivation of response functions of G_V to the full range of meteorological drivers, accounting for interactions and confounding factors, requires more rigorous statistical analysis, which is provided in the next section on response functions.

2.4.9 Climate response functions for canopy conductance

The statistical analysis of the response of G_V to climate drivers utilized data for May 19-November 10, 2001, the period of available data for all eddy covariance towers simultaneously. This covered the period of the mature canopy unstressed activity through the summer dry-down and senescence before the first winter rains. Data examined were those for which the flux was positive and during which incoming PAR was greater than 50 W m^{-2} ; these constraints effectively removed nighttime data. These statistical analyses were performed only on eddy covariance data and not on the sap flow data, since the climate drivers corresponded to the exact same times as the eddy fluxes, whereas with the sap flow data, the timing of drivers could not be precise.

Results from ACE non-linear transformations are shown in Figure 2.31 for G_V as derived from the eddy covariance towers. The associated curve fits on the ACE transformations and regression statistics are tabulated in Table 2.7.

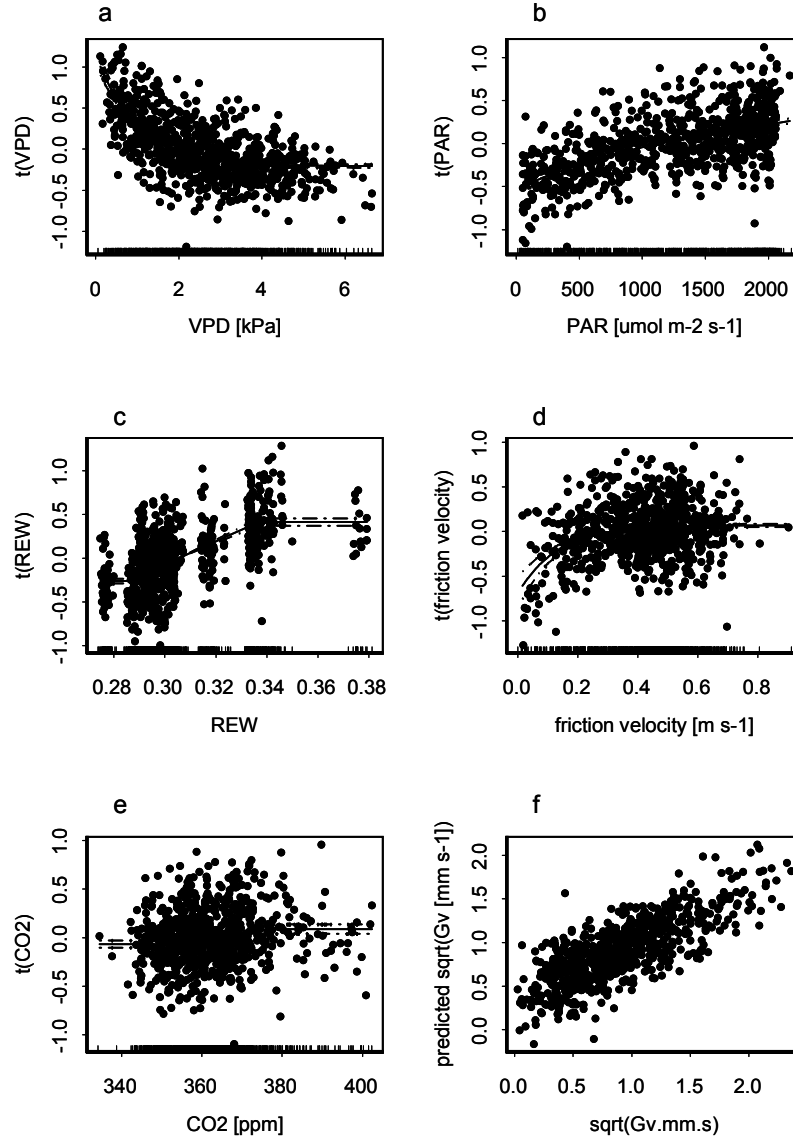


Figure 2.31: Partial residuals for least-squares regression on canopy conductance, G_v (variance stabilized with sqrt) vs. transformed controlling variables, VPD, PAR, REW, u_* , and CO_2 . $R^2 = 0.60$ compared to null model R^2 of 0.51. Hatchmarks along the bottom axis occur below their respective datapoints to illustrate the density distribution of the data. Dashed lines show pointwise 95% confidence intervals. Ione savanna, 2001.

variable	transformation	deviance	std. error (t value)	Pr(> t)
G_V [mm s ⁻¹]	$\text{sqrt}(G_V)$	–		
VPD [kPa]	$1.37 \exp(-VPD) - 0.21$	143	0.03 (19.2)	0.0000
PAR [umol m ⁻² s ⁻¹]	$-1.1 \exp(-0.0006 PAR) + 0.58$	112	0.03 (17.7)	0.0000
REW [fraction]	piecewise linear, breakpoints at REW = 0.34 and 0.28 slopes and intercepts are: 0, -0.32 [REW=0 to 0.28]; 13, -4.0 [REW=0.28 to 0.34]; 0, 0.42 [REW=0.34 to 1]	70	0.03 (19.3)	0.0000
friction velocity, u_* [m s ⁻¹]	$-0.76 \exp(-7.4u_*) + 0.068$	66	0.05 (7.9)	0.0000
CO ₂ [ppm]	$0.071 * \tanh(0.1 * (CO_2 - 330) - \pi) + 0.005$	64	0.09 (3.6)	0.0004
Intercept	0.89		0.01 (82.5)	0.0000

Table 2.7: Response functions and regression statistics for eddy covariance canopy conductance, Ione savanna, 2001. Multiple R-Squared = 0.594. Null deviance 158.4 on 746 degrees of freedom. Residual deviance 64.4 on 741 degrees of freedom

The eddy covariance conductances were found to maximize correlation to the climate drivers with respect to the square root of the conductances, a common transformation that stabilizes variance for Gaussian distributions about the mean. The fact that a log transform of G_V does not provide a better fit to these data implies that these response functions cannot be used in a multiplicative manner. This does not mean that a Jarvis-type model could not be fit to these data, but that such a model form would not fit as well. Therefore, a simply generalized additive model is examined. The transformations shown here are therefore not scaled between 0 and 1, and are related to $\text{sqrt}(G_V)$; therefore note that the units on the y-axes are not flux units, but some scaling of flux units. What is important to observe are the non-linear trends, asymptotes, optima, and breakpoints relative to the original climate driver. Also important to observe are where certain combinations of

conditions do not occur (e.g. simultaneous high temperature and soil moisture), such that a mere statistical analysis of real conditions cannot always provide information on important critical points and thresholds.

For canopy conductance as derived from eddy covariance data, the significant drivers ($p < 0.01$) were found to be vapor pressure deficit (VPD), photosynthetically active radiation (PAR), and soil moisture (REW for whole soil profile). Friction velocity was significant at $p < 0.05$, and CO_2 concentration was not significant at $p < 0.3$. CO_2 was included in this analysis, since it exhibits clear diurnal and seasonal trends (declining in the afternoon and also declining over the summer), but apparently it is only a weak driver compared to the other variables. For the eddy covariance transformations, VPD exhibits the expected exponential reduction effect on G_V (Figure 2.31a). Because air temperature was so nearly linearly correlated with VPD, temperature and VPD were not both significant when both included in the statistical model; therefore, only VPD was kept for the sparse model. The PAR response barely exhibits light saturation, most likely because conditions are never non-stressed with respect to soil moisture or VPD such that light saturation is rarely achieved. Friction velocity was an important variable to include, to account for effect of wind speed on the eddy covariance measurement technique (Figure 2.31d). The ACE diagnostics clearly revealed a cut-off point of about 0.3 m s^{-1} , above which the eddy covariance measurements are not adversely affected by wind speed. Although nighttime values were eliminated from this analysis, there are still obviously daytime periods with low wind speed. Friction velocity can thus be considered a confounding variable that researchers must account for in estimating canopy conductances from eddy covariance data.

Soil moisture accounted for the third largest amount of the model deviances among all the variables for eddy covariance data, and the ACE transformations discerned what appear to be important breakpoints for the onset of water stress ($REW=0.34$) and senescence ($REW=0.28$) (Figure 2.31c, and equation in Table 2.7). Note that these REW values are for the entire soil profile to 0.55 m deep, whereas the soil layers most available to the blue oak trees are in the upper 20 cm. The REW for the entire profile was kept, since choosing a cut-off would have been somewhat arbitrary, and it is intended later to consider how the total water in the soil system could be related the optimal usage of water by the vegetation. If REW were calculated only for the upper 20 cm of soil, then the REW critical points in this regression would be lower, of course.

CO_2 concentration exhibited asymptotes in an S-shaped response in its influence on variation in canopy conductance, tailing off at minimum at about 350 ppm and saturating at about 380 ppm. Of all the variables, it had the smallest influence on canopy conductance with little significance at $p<0.3$. Temporal plots of CO_2 showed a consistent decline in CO_2 concentration during the day. Given the larger scatter of the partial residuals for CO_2 , the weak correlation of G_V with CO_2 and the asymptotes found may be due to correlations with other diurnal phenomena. The curve fit for CO_2 does not provide a better fit than a null linear model, so it may be concluded that CO_2 concentration is at least positively correlated with conductance, while the existence of saturation points remains an area of speculation.

As with any statistical model, there are caveats. The response functions that have been uncovered in this generalized additive model are merely a description of patterns found

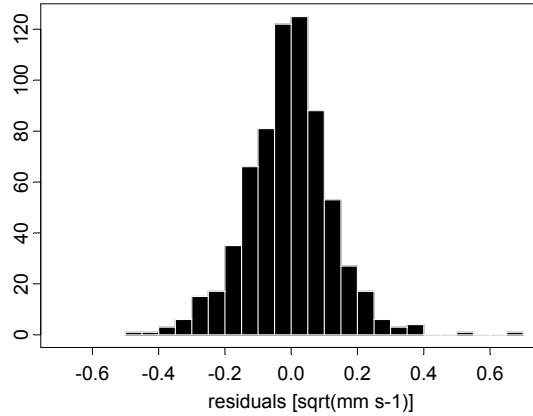


Figure 2.32: Histogram of the residuals of the generalized additive model fitted for the responses of canopy conductance. Shows a Gaussian distribution. Ione savanna, 2001.

within the range of data and are therefore limited by that range. If the range of the driving variables does not span where they would not restrict conductance, then a multivariate regression cannot discern what the response would be in that region. In the data here, the meteorological drivers, light, vapor pressure deficit, wind speed, span a wide range, but soil moisture is rarely above unrestricted levels, and blue oak leaf area was difficult to quantify during the period of senescence. Therefore, there is more scatter in the fit in times of higher soil moisture, and oak leaf area data could not provide a strong enough range to fit a response.

With respect to the model fitting within a Gaussian distribution of errors, the model does well, as shown by the histogram of residuals in Figure 2.32. However, since the model is treating time series data as independent observations, it does not account for the possibility of autocorrelations. Figure 2.33 shows what appears to be sinusoidal autocorrelation at the scale of one day. Spikes occur where the sample size is small for a particular

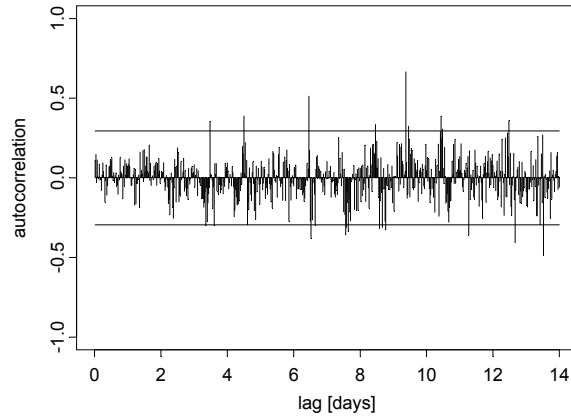


Figure 2.33: Autocorrelation function of the residuals with lines indicating one standard deviation for the generalized additive model of canopy conductance at the Ione, CA, savanna, 2001. Shows sinusoidal autocorrelation at the time scale of one day. Large spikes occur where there is a very small sample size.

lag, leading to a poor estimate of the autocorrelation, and in general the autocorrelation estimate is poorer for longer lags, hence the lack of damping in the autocorrelation plot. Except for small-sample spikes, the autocorrelations fall within a standard deviation and can be considered small, but the underlying noisy sinusoidal pattern implies that a better fit could be achieved, perhaps, with a model that parameterizes the meteorological drivers as times series functions. Overall, however, the functional responses fit in the generalized additive model will not change, since they represent strong trends within the variation of the data.

This analysis of climate response functions provides a useful descriptive breakdown of influences on canopy stomatal conductance, but it is not sufficient yet to explain those responses. For example, the blue oak critical points were identified for response of conductance to soil moisture, thus quantifying water use characteristics for the physiognomy

(i.e. root-stem-leaf hydraulic pathway and drought tolerance) of this species, but the plant physiognomy must explain those critical points. Also, because focus here was specifically on meteorological and soil moisture drivers, the influence of plant biochemistry was not included. Leaf gas exchange measurements by Xu and Baldocchi (2002, submitted) on a blue oak at the Ione savanna site show clear seasonal trends in leaf photosynthetic capacity (Figure 2.34, upper graph, maximum carboxylation capacity, $V_{C\max}$), which are repeated by leaf stomatal conductance (Figure 2.34, middle graph). The bottom graph of Figure 2.34 shows that these trends correspond to a summer decline in leaf nitrogen content. The peak in blue oak stomatal conductance, g_s , occurs in early May 2001 (approximately Julian day 125). This is at the same time as the beginning of grass senescence, and just before the measured soil moisture reaches its threshold low values. Photosynthetic capacity, $V_{C\max}$ (calculated following Harley, et.al., 1992), peaks later than g_s by about 25 days (at the same time when air temperature first reaches its maximum for the summer. Thereafter, $V_{C\max}$ declines throughout June and appears to stabilize at a lower level for July-August, even while the blue oaks' leaves are gradually senescing (fitted line is through local regression, S-Plus 2000 software by MathSoft, Inc.). Comparisons of these values to that of other species in other climates are detailed in Xu and Baldocchi (2002, submitted). Given that limitations on carbon assimilation rate also limit leaf stomatal conductance (Farquhar and von Caemmerer, 1982; Ball and Berry, 1987; Collatz, et.al., 1991), a variable like $V_{C\max}$ should be included in an analysis of response of G_V . However, one can then ask the question whether plant biochemistry (e.g. leaf nitrogen content or photosynthetic capacity) and plant functional form (e.g. rooting depth, hydraulic conductivity) should be considered

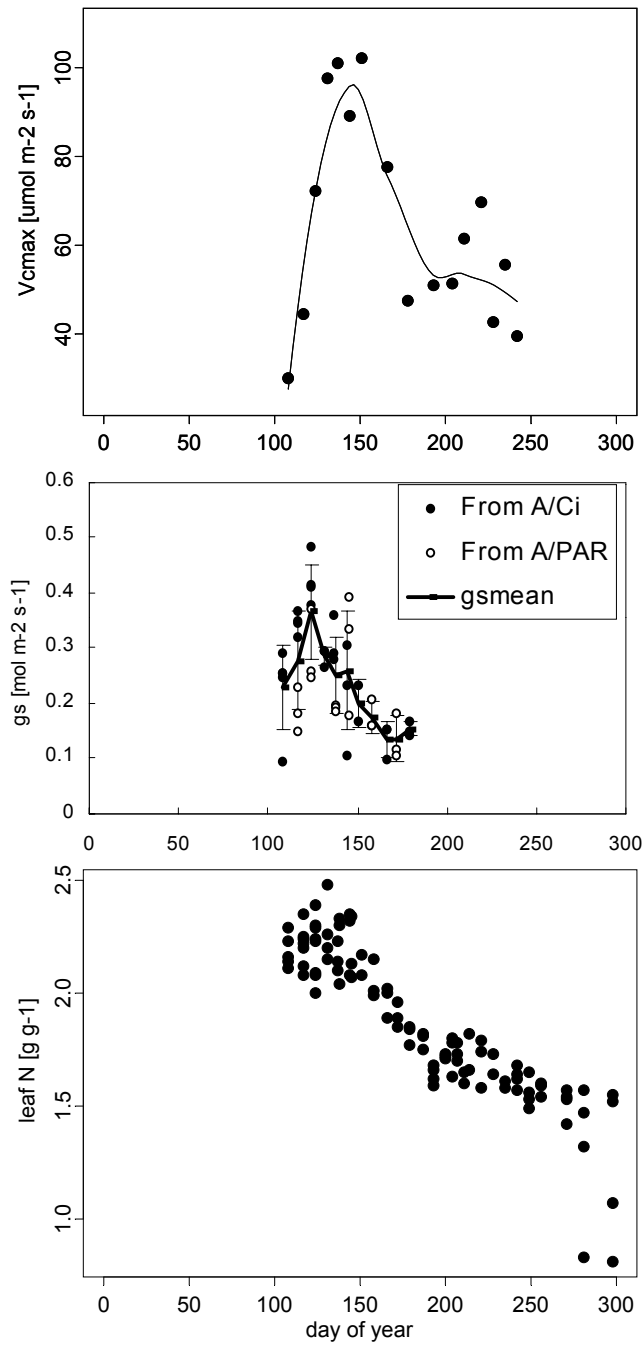


Figure 2.34: Seasonal trends in blue oak (*Q. douglasii*) leaf parameters: upper graph, maximum carboxylation capacity, V_{Cmax} ; middle, stomatal conductance, g_s ; bottom, leaf nitrogen content. Ione savanna, 2001 (source: Xu and Baldocchi, submitted).

as independent drivers of canopy stomatal conductance, or as results themselves of climate drivers. It is proposed here that the answer lies somewhere between. Canopy stomatal conductance is a function of immediate meteorological and soil moisture conditions as well as the bounds imposed by plant biochemistry and functional form. These latter two are results of long-term adaptations to the broader climate of the landscape. To determine these plant traits directly from climate statistics then is another area of research (potential vegetation and optimality models, e.g. of Osborne, et.al., 2000; Kergoat, 1998; and Kiang, this dissertation, solving for potential $V_{C\max}$ given climate).

Does the vegetation at the Ione savanna behave as would "potential vegetation?"

This question is examined next with regard to actual and potential water usage of the system.

2.4.10 Actual vs. potential evapotranspiration

The ratio of actual evapotranspiration (AET) to potential evapotranspiration (PET) is a useful, water balance approach to quantify when vegetation begins to experience soil moisture deficits, and to discern how well different vegetation functional types may be coordinated to fully utilize available energy with respect to transpiration. Figure 2.35 shows PET above the Ione savanna tree canopy and the open grassland site as estimated with the Priestley-Taylor equation, combined with AET as measured by the three eddy flux towers above and below the tree canopy and over open grassland. The upper edge of each area plot is an envelope for the smoothed (local regression, S-Plus, MathSoft) maximum instantaneous values for each day (note that the sharp vertical line at the beginning of each area plot indicates where each data record begins in time). The normalized relative

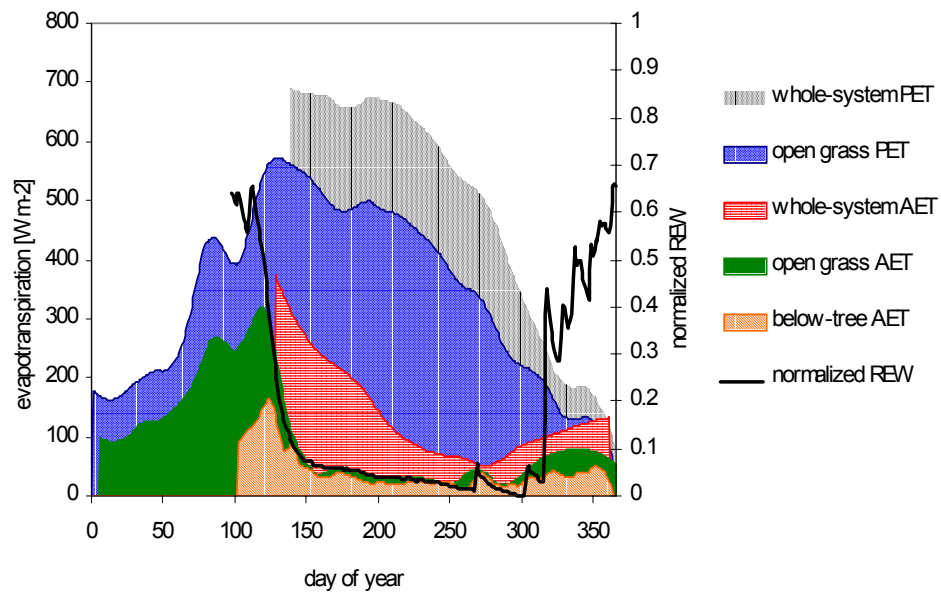


Figure 2.35: Actual evapotranspiration (AET) from eddy covariance measurements of latent energy fluxes, overlaid with potential evapotranspiration (PET) estimated by the Priestley-Taylor equation. Relative extractable water (REW) shows coinciding decline in understory AET, while overstory AET persists through summer. Ione savanna, 2001.

extractable water (REW) (thick line, normalized for visual purposes, so that the minimum value is zero) is included on this figure to show how the understory decline in AET corresponds with the soil moisture dry-down rate, whereas the trees are able to persist through the summer through various drought tolerance mechanisms. Note that in comparing the understory AET and PET, distinction cannot be made between soil and grass fluxes in the eddy covariance data. However, it is possible to distinguish the tree layer alone.

In the wet winter, temperature but not water limits evapotranspiration, while vegetation controls further influence the amount of evapotranspiration (leaf area, stomatal control). The grassland AET matches the trends in PET, though not quite the magnitude, until about Day 115, when rains have ceased and the soil begins to dry, after which the understory AET declines rapidly over the short spring. In the summer, obviously, soil moisture but not temperature is limiting to transpiration; notably, the oaks, through drought tolerance mechanisms, are able to maintain a steady linear decline in transpiration, rather than an exponential decline as exhibited by the pine and understory. The different vegetation cover types also influence the available energy as well as being influenced by it: during the dry summer, the PET for open grassland is less than that for the tree canopy, because lower net radiation results from greater losses of sensible heat over dry soil, in contrast to higher net radiation from the heat absorption by the tree canopy and boles. With the arrival of fall rains, there is surplus moisture while PET is low. That the grassland AET does not achieve PET even though water is not limiting leads us to ask why this system does not appear to maximize its utilization of the available water and energy: are there biochemical constraints? Could grazing severely reduce leaf area in the winter as to

reduce transpiration?

The blue oaks leafed out beginning on Day 81 (March 22), after which they required till Day 140 (April 20) to acquire a full, mature canopy of leaves (see Figure 2.13), a day which coincides with senescence of the understory grasses. Unfortunately, the overstory eddy covariance tower was not fully operational until Day 127 (May 7), such that measurements missed the period of early spring leafing out; however, there is evidently a very narrow time window within which the trees only briefly, if at all, experience a period of soil moisture saturation when the tree canopy plus understory AET might match PET. Since the tree canopy achieves only an average LAI of 0.6, one would expect the trees' AET to be limited during the summer and that the low LAI and open canopy are reflections of soil moisture restrictions on plant cover. It is interesting to observe that the tree bud burst is coordinated with the grass dry-down and senescence to take over ecosystem functioning. Such apparent coordination among plant functional types hints at evidence of optimization of the system for utilization of available water and energy resources, yet also prompts questions about why PET is not achieved when water is not limiting in this system.

To more exactly quantify when the tree AET/PET is limited by soil moisture, this ratio is regressed versus REW in Figure 2.36 (local regression, S-Plus, MathSoft, Inc., smoothing span=0.6). The relation between AET/PET and REW exhibits a distinct linear trend from the lowest available REW to about REW=0.36, staying approximately constant above this value through REW=0.5, and then declining above REW=0.6. The strong linearity up to REW=0.36 and plateau are in accord with the response to soil moisture stress as observed by Gollan, et.al. (1985), and as modeled by hydrologists Rodriguez-

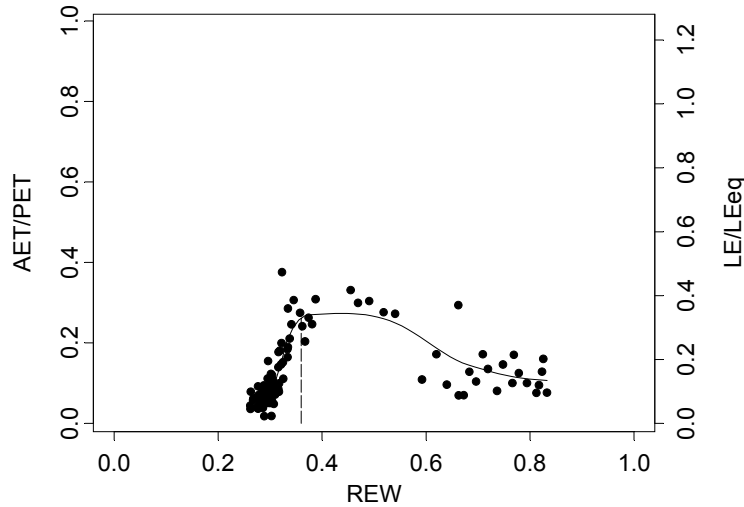


Figure 2.36: Tree AET/PET vs. relative extractable water (REW). Vertical dashed line indicates where $REW = 0.36$. Left axis: AET/PET. Right axis: LE/LE_{eq} , same as multiplying AET/PET by Priestley-Taylor factor of 1.26. Ione savanna, 2001.

Iturbe, et.al. (2000). The decline above $REW=0.6$, however, occurs in this data set, as these higher REW values happen during the late fall rains at the Ione savanna site, when the trees have largely senesced and when V_{cmax} is very low, such that AET is limited by leaf area and photosynthetic capacity. The data for 2001 do not cover a period of simultaneous high REW and full tree canopy, but it can be hypothesized that future data covering such a combination of conditions will result in a more continuously horizontal plateau in AET/PET at high REW. It may also that the Ione oaks never experience very wet conditions during their growing period, due to the phenology of the blue oaks, whose budburst does not happen until after the winter rains are over and the soils are already beginning to dry down.

Examining just the data below $REW=0.6$, the onset of stress appears to occur at

REW=0.36, with a maximum AET/PET between 0.3 and 0.4. The critical point of 0.36 is close to the value of 0.34 detected by the ACE algorithm. The value of 0.36 REW corresponds to a volumetric water content of 0.12, which is the wilting point conventionally predicted at a soil moisture potential of -1.5 MPa by the model of Saxton, et.al. (1986) (refer again to Table 2.1). The blue oaks, as was seen earlier, can function at potentials down to -4.5 MPa or lower, and the Ione savanna trees did not begin senescing until leaf twig water potentials lower than -3.5 MPa (mid-July). Therefore, REW=0.36 is not the wilting point of the blue oaks, but it is clearly a critical point in their transpiration behavior, as something is altering physiologically in the oaks, perhaps cavitation of hormonal signals, the drought responses whose mechanistic explanations as yet elude scientists.

In a closed canopy system, AET/PET would ideally be 1, unstressed, at REW greater than the soil moisture stress point. In reality, even ecosystems that are not water-stressed ecosystems vary in the maximum ratio they are able to achieve, dependent on vegetation functional type (surveyed by Valentini, et.al., 1999). For whole ecosystem fluxes, Valentini, et.al. (1999) calculate the ratio of latent energy flux, LE, to equilibrium latent energy, LE_{eq} (where LE_{eq} is the Priestley-Taylor function, excluding multiplication by the Priestley-Taylor constant of 1.26, such that $LE/LE_{eq} = 1.26 \cdot AET/PET$). LE/LE_{eq} is calculated for the Ione savanna, both trees and grass, versus REW in Figure 2.37 (fitting a line through local regression as before). Like the tree-only fluxes, the full-system fluxes exhibit a strongly linear response to soil moisture under stressed conditions, peaking at a higher REW (approximately 0.5), and then declining at higher REW, due, again, to the fall rains covered in this dataset. The Ione savanna's maximum values of $LE/LE_{eq} \sim 0.8$

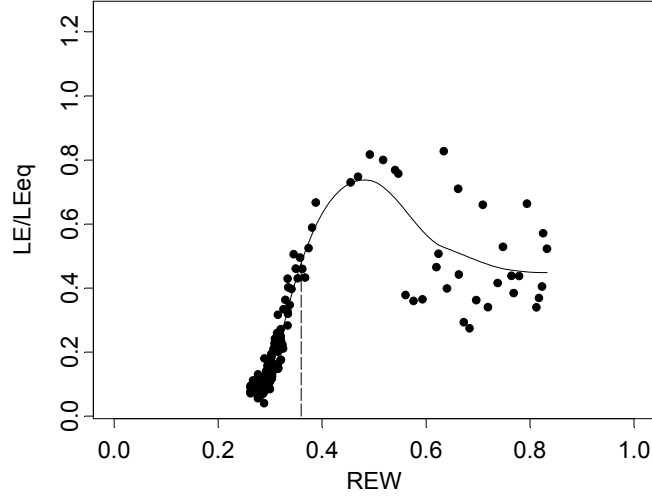


Figure 2.37: Ecosystem LE/LE_{eq} for the Ione savanna, 2001. Dashed vertical line indicates $REW=0.36$, stress point for the trees.

are close to those surveyed for cerrado (0.82) (Valentini, et.al., 1999, citing Miranda, et.al., 1996), out of a range of 0.37 to 1.5 for all ecosystems.

2.5 Conclusions

A variety of measurements were performed of seasonal trends of this California blue oak savanna and its components: leaf area index, tree leaf twig water potential, soil moisture, tree hydraulic conductance, tree canopy conductance, and evapotranspiration of the understory and tree layers as measured by sap flow and eddy covariance. In addition to adding to the database on magnitudes of fluxes for a semi-arid ecosystem type, this is the first, continuous horizontal and vertical partitioning of flux contributions by the tree and grass layers in a savanna, and the response of tree canopy stomatal conductance to soil

moisture was identified. Tree transpiration was examined in the context of bulk measures, such as hydraulic conductance; through exploratory hysteresis and stratified response curves of canopy stomatal conductance to vapor pressure deficit and light; and finally through a rigorous multivariate diagnosis of the forms of canopy stomatal conductance responses to all potential meteorological drivers and their interactions. Note that this analysis only included variables related to climate and not related to plant biochemistry. Finally, the trends in the actual evapotranspiration of the different ecosystem components were examined compared to the potential evapotranspiration and considered how the grass and tree functional types trade off with each other to maintain ecosystem activity throughout the winter through summer seasons.

2.5.1 Measurement technique

The sap flow measurement required only a few trees to scale up by sapwood area to the landscape scale for the Ione savanna, since sap flux density is fairly uniform across tree sizes in this open-canopy ecosystem. The heat pulse method works very well during the summer dry period but is most likely missing peak flow in the outer xylem vessels in the spring due to disruption of growth of largest vessels by the sensors, or too close correspondence in scale between the vessel diameters and the sensor diameters. Sap flow measurement appears a good means to corroborate eddy covariance, but it is unclear if the heat pulse technique (or any other needle probe technique) can be fixed to capture the missed peak flow in a ring-porous tree, since outermost xylem vessels are most susceptible to cavitation, disruption by the needle sensors and to environmental noise. Eddy covariance in the understory seems to perform satisfactorily for an open canopy, and the estimation of

tree-layer transpiration from differencing between the overstory and understory eddy flux measurements seems to provide reasonable accuracy, as evidenced by convergence with the summer fluxes measured from sap flow. Refinements to this patch-type averaging of under-tree and open grassland areas could be addressed further by positioning an understory eddy covariance system in the open directly at the savanna site, rather than using the data from the open grassland site.

2.5.2 Tree transpiration responses to climate drivers

The forms of the responses of canopy conductance, G_V , to the usual controls, VPD, PAR were readily discerned by the ACE algorithm. In addition, the friction velocity influence on eddy covariance measurements was accounted for by this regression technique, with a threshold found at 3 m s^{-1} . Weak correlation was found with CO_2 concentration. Most importantly, response of canopy stomatal conductance to soil moisture (REW) was found highly significant, and critical stress points were found, both by the ACE algorithm and by inspecting the ratio of AET/PET versus REW. These stress points were found to be at REW values of 0.34 for the onset of stress and 0.28 for the onset of wilting. A multiplicative Jarvis-type model was not found to be the best statistical model for analysis of this data, as the conductances were better related by their square root to the predictor variables, than by their log. This statistical analysis was useful for identifying important critical points and the forms of non-linear responses. Meanwhile, an examination of LE/LE_{eq} yielded a maximum value, 0.8, the same as that found for a cerrado (Miranda, et.al.1996), lending support to a consistent functionality among savanna-type ecosystems. That there is a strongly linear decline with soil moisture deficit in these actual versus po-

tential ratios inspires questions about why that decline is linear? Also, what is keeping the actual fluxes consistently lower than the potential? Could nutrients be limiting $V_{C_{max}}$ in this system? The leaf gas exchange measurements by Xu, et.al. (2002, submitted) showed the maximum carboxylation capacity of Rubisco, $V_{C_{max}}$, of the oaks to vary seasonally, with a brief peak in the spring and then steady decline throughout the summer. Since stomatal conductance is also a function of carbon assimilation rate, which is a function of photosynthetic capacity, this latter quantity should be considered as another confounding variable in analyses of drivers of canopy stomatal conductance. However, it is a species-specific parameter that is difficult to obtain on a wide scale, just as it is difficult to obtain measures of plant hydraulic conductivity, and the purpose here is to identify climatic drivers of conductance. Since biochemical parameters like $V_{C_{max}}$, and anatomical characteristics like hydraulic conductivity reflect plant adaptation to climate (Woodward, 1987), ideally, it is desirable to obtain these values from climate statistics as well. Such a goal lies in the realm of ecological optimality theories and the definition of functional types in vegetation.

2.5.3 Coordination of functional types

The out-of-phase phenology of the oaks and the annual herbaceous understory and their timing with respect to soil moisture generate many hypotheses about the optimal coordination of the different plant functional types to utilize available water and energy over the course of the different seasons. Phenomenologically it is observed that the grasses leaf out with fall rains; then grasses senesce simultaneously with bud burst of the oaks during period of rapid soil dry-down; and finally the oaks gradually senesce over the end of the summer. Quantitatively, the monitoring at Ione of both herbaceous and tree fluxes shows

what appears to be coordination among the functional types for maximal utilization of available resources (water, energy): actual evapotranspiration by the grasses closely tracks the trends of potential evapotranspiration in the wet winter (but consistently remains below potential values); and then grass senescence is followed by oak maintenance of transpiration over the course of summer drought, with actual evapotranspiration limited below potential due to soil moisture; however, the drought-tolerance behaviors of the oaks allow them to maintain a steady linear decline in transpiration, rather than following the exponential decline of soil moisture as exhibited by the pines and understory.

The drought avoidance behavior of the grasses versus the drought tolerance behavior of the oaks leads us to ask why each particular functional type is better suited to its particular growth seasons, and why the pines persist throughout the year. How much is the functional differentiation due to water use strategy (rooting depth, biophysics of water transport and leaf gas exchange), or temperature influences on growth form, or biochemical constraints for different seasons? These properties are functions of long-term adaptations to climate, and the matching of the relevant parameters to climate continues to be an area of research in optimality models, such as rooting depth in models of ecohydrological equilibrium (Rodriguez-Iturbe, et.al, 2001), or potential carboxylation capacity in a biophysical potential vegetation simulation model (Osborne, et.al., 2000), or the simultaneous solution for such vegetation functional parameters in a stochastic optimal control representation of canopy stomatal conductance (Kiang, this dissertation). In the blue oak savanna, the ring-porous anatomy of the blue oaks causes them to experience "frost drought", because freezing embolisms during the winter prevent conductance of sap through the xylem vessels,

while the grey pines are able to persist during the winter, because the individual tracheids are easily recharged following rain and do not pass the embolism gas bubbles to others (Woodward, 1987). While the pines can grow through the winter, the broad-leaved blue oaks are better able to maintain productivity during the warm, dry season, a differentiation that is observed also at global scale with regard to temperature limits and productivity (Woodward, 1987). Why the grasses exhibit annual behavior, senescing before the summer to avoid drought, might be explained by rooting depth; however, it should be recalled that these annual grasses are invasive species since Spanish colonization in the 18th century, whereas the native grasses were in fact perennial with deep rooting depths (Barbour and Major, 1988). Therefore, it is unclear whether annual or perennial behavior in the understory provides for maximal utilization of resources (many other ecological issues are involved with respect herbivory, as mentioned in the introduction to this chapter). That the evapotranspiration of the grasses in the wet winter is consistently below potential values requires us to ask what is causing this limitation. Is temperature limiting photosynthetic activity? Is grazing limiting leaf area index? Are nutrients limiting photosynthetic capacity? Is this system indeed at equilibrium with climate or is it still developing toward that state?

2.5.4 Future research

Given these patterns of water and energy supply and usage, the next question to ask is whether the CO₂ uptake is optimal as well: are leaf area, stomatal conductance, and photosynthetic capacity coordinated with water loss in such a way as to maximize uptake of CO₂ (or some other measure of productivity or fitness) within the climate constraints?

Answering of this question is less straightforward than for evapotranspiration, since carbon assimilation is dependent on species-specific biochemistry, and net productivity is also a function of respiration and below-ground allocation. To investigate whether the biochemical characteristics of vegetation at the Ione savanna site conform to some type of optimization under climate constraints, productivity measures (e.g. gross and net primary productivity) should be extracted from the eddy flux measurements (Figure 2.38 shows the 7-day moving averages of net CO₂ fluxes, which do not differentiate photosynthesis and respiration) and see how these compare to "potential productivity" as in a model like that of Osborne, et.al. (2000) and Kiang (in preparation, this dissertation). Soil and bole respiration data being collected by other researchers will eventually allow partitioning of the carbon fluxes both between tree, grass and soil layers, and between photosynthesis and respiration; and future optimality modeling is forthcoming.

The tools are now available to quantify the fluxes of water vapor, carbon dioxide, and energy between natural ecosystems and the atmosphere; the ability to partition the components contributing to these fluxes; and the frameworks for identifying responses of canopy stomatal conductance to immediate meteorological drivers. Continued measurements at this site should investigate further the contribution of hydraulic lift in this system (Dawson, 1996), and refine the sap flow measurements to quantify the contribution of tree bole capacitance (i.e. sensors at different heights on a bole to measure storage). The continuing and future measurements of respiration and transpiration will allow more refined estimations of a carbon budget for this system, as well as observation of system responses to interannual climate variability.

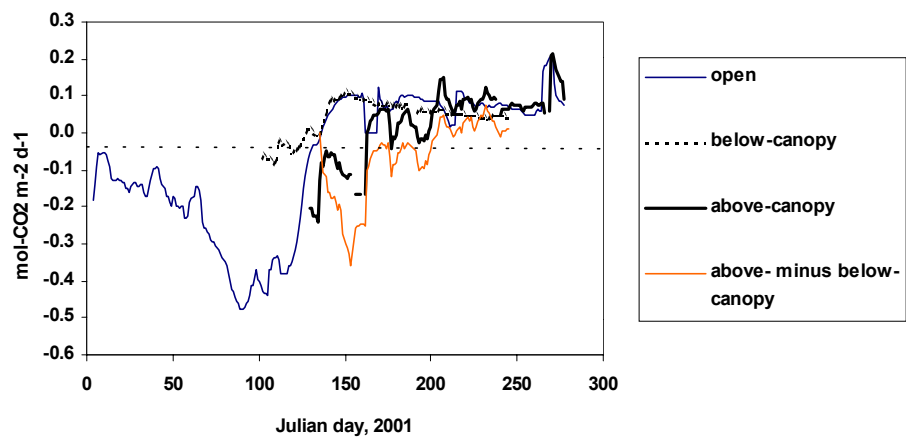


Figure 2.38: 2001 trends in daytime CO₂ fluxes (7-day moving averages) in open grassland, below tree canopy, and above tree canopy environments of blue oak savanna, Ione savanna and grassland sites, 2001.

Chapter 3

Ecohydrologic optimality: The soil moisture balance and water stress in a Mediterranean oak savanna

Summary: Predictions are presented here of soil moisture for a Mediterranean savanna ecosystem using the ecohydrological equilibrium theory of Rodriguez-Iturbe and co-workers' (Rodriguez-Iturbe, et.al. 2001; Laio, et.al., 2001a; Laio, et.al., 2001b). This theory has yielded intriguing theoretical insights into the role of water stress in structuring vegetation communities in arid ecosystems (Laio, et.al., 2001b). Here, the theory is examined more closely for the tree and herbaceous savanna vegetation in a Mediterranean climate, which differs from previously tested ecosystems, because temperature and precipitation are seasonally out-of-phase in this type of climate, and also the two different vegetation functional types have different growing seasons. Seasonal periods are distin-

guished based on climate and vegetation function, and the probability density functions (pdf's) of soil moisture and values of dynamic water stress are generated. These pdf's are then compared to actual soil moisture data and lend support to root depth studies (Millikan and Bledsoe, 1999), matching closely parameterizations for grass dominant root densities in the upper 20 cm of soil and oak root densities in the upper 50-60 cm. Finally, the seasonal behavior of this Mediterranean savanna is discussed in comparison to those examined by the original researchers. Suggestions for the advancement of the ecohydrological theory are made to account not only for precipitation but also for the timing of available energy and plant productivity.

3.1 Introduction

The correlation of vegetation types with climate has long been documented through extensive global surveys, maps, and satellite data (Holdridge, 1967; Whittaker, 1975; Defries and Townshend, 1994), correlations which climatologists have replicated with some success through computer simulations based on ecophysiological theories of limiting water resources (Aber and Melillo, 1991; Nemani and Running, 1989; Woodward, 1987; Neilson, 1995; Haxeltine, et.al., 1996; Foley, 1996; Prentice, 1992). The meaning here of "climate" is that of a long-term statistical characterization of the temperature, precipitation, and general weather patterns of a region. Because of these relations to climate and the desire to predict vegetation-climate interactions, the classification of "vegetation type" has evolved toward definitions of functional attributes, morphological and behavioral features of a plant that clearly distinguish it from others in its response to climate and weather, such

as woody versus herbaceous, needle-leaved versus broad-leaved, deciduous versus evergreen, etc. (Defries, et.al., 1995). As such research has been the work of plant ecophysiologicalists and atmospheric climatologists, the role of soil has received short shrift in the equilibrium theory, and it is where soil moisture is limiting that accuracy is poorest in these models.

In contrast, hydrologists have focused on soil processes with little attention to the role of vegetation in controlling the fluxes of water from the soil to the atmosphere. Just a few researchers have worked on advancing the field further in this respect, the most notable being Peter Eagleson, and Ignacio Rodriguez-Iturbe and co-workers. Peter Eagleson (1978abcdefg; 1982; Eagleson and Tellers, 1982) asked the critical question: should not both soil and plant properties co-evolve toward some equilibrium values with climate? Given just climate, can we predict the soil and vegetation mix? Eagleson devised a theoretical model based on annual precipitation, in which he derived analytic long-term equilibrium solutions of soil moisture holding capacity, vegetation cover, and vegetation "transpirativity," based on an overall ecosystem development direction toward zero run-off, minimization water demand stress, and all moisture being utilized by the vegetation. Based on root depth partitioning of soil moisture, he made predictions of the relative cover of woody versus herbaceous vegetation in two savannas (Nylsvley, South Africa; Jonglei Canal, Sudan), which remarkably fall upon his non-dimensional relation between woody cover versus the ratio of soil "evaporativity" and vegetation transpirativity. Eagleson's work, unfortunately, has had little follow-up by subsequent researchers (Hatton, et.al., 1997), perhaps because of its voluminous presentation in an entire issue of *Water Resources Research* (1978abcdefg), or because as an intellectual investigation of long-term equilibria, it not immediately useful

to most hydrologists who are concerned with quantifying fluxes of water. Also, as zero run-off occurs in few ecosystems, there is the question as to whether this is a true optimality criterion or if somehow run-off must be accounted for in the theory. Nevertheless, Eagleson's work is important for framing the fundamental question of ecohydrology: the coevolution of soil and vegetation characteristics with climate to achieve some optimal utilization of water resources.

Rodriguez-Iturbe and co-workers (Rodriguez-Iturbe, et.al., 2001; Laio, et.al., 2001a; Laio, et.al., 2001b; Porporato, et.al., 2001) decided to introduce hydrologists' water balance modeling to further the ecohydrological optimality theory. They derived a probabilistic model of soil moisture balance based on hydrologists' classic statistical techniques for representation of climate. The soil moisture balance model distinguishes itself from previous hydrologists' work by incorporating a description of vegetation response to water stress: plant transpiration declines linearly with soil moisture deficit. Their rationale draws from evidence by meteorologists that evapotranspiration declines linearly with soil moisture deficit in the field (Brutsaert and Chen, 1995, 1996), by plant physiologists who observed the same phenomenon in leaf gas exchange measurements in the laboratory (Schulze, 1986), and by ecophysiologists working on sap flow in trees (many). The model of Rodriguez-Iturbe and co-workers predicts probability density functions of soil moisture (Laio, et.al., 2001a), which then become tools for calculating various measures of water stress in an ecosystem, such as the probabilistic time rate of transience from one soil moisture state to another, and the level of water stress that plants can expect to experience over a period of time (Porporato, et.al. 2001). These measures can be viewed as more refined

water balance indicators to explain various features of the vegetation in an ecosystem, such as the rooting depth, the different water use strategies of different species in the vegetation mix, and functional characteristics such as perennial versus annual behavior (Laio, et.al., 2001b).

The model of Rodriguez-Iturbe and co-workers is good for asking, given climate, soil characteristics, and vegetation characteristics, can we explain the vegetation mix? I.e. how is vegetation adapted to the climate and soils? Therefore, their model addresses a subset of the overarching ecohydrological question framed by Eagleson, in that they frame the stochastic relations between *current* vegetation, soil, and climate, rather than their long-term equilibrium evolution toward total useage of water resources. For example, Rodriguez-Iturbe and co-workers (Laio, et.al., 2001b) applied their probabilistic soil moisture equilibrium model to data from two savannas and a grassland: a tropical warm savanna in Nylsvley, South Africa (Scholes and Walker, 1993), a brushland savanna in La Copita, Texas, and a short-grass steppe in Colorado. They calculated the soil moisture pdf's for these sites with different rainfall regimes and soil textures, and for species with different rooting depths and water use strategies, and compared stress levels for the different species. These characterizations yielded interesting insights into the tree-grass coexistence in savannas and the grass distribution in the short-grass steppe. In Nylsvley, similar rooting depths of two woody and two herbaceous species but different water use strategies (level of maximum transpiration rate, stress and wilting points) yield the same average water stress levels for each species over their growing season, thus affording their coexistence in a savanna. At La Copita, interannual variation in climate leads to fluctuation in the com-

petitive advantage (trade-off in stress levels) between trees and grasses, leading to unstable coexistence. In Colorado, the short-grass species *Bouteloua gracilis* was shown to prefer different soil textures for different rainfall regimes. The researchers conclude with avenues for future research to account for the roles of productivity, interannual climate variation, and the evolutionary dynamics of vegetation.

Eagleson and Rodriguez-Iturbe tested their theories by predicting vegetation cover or distinguishing vegetation functional types in their water use strategies. They had special interest in savannas, because water limitation is a characterizing feature of these ecosystems (Walter, 1971; Scholes and Archer, 1997). Here, a first application of Rodriguez-Iturbe, et.al.'s (2001) theory is performed for a Mediterranean ecosystem, examining closely the role of seasonal variation. The seasonal soil moisture pdf's are calculated from Rodriguez-Iturbe, et.al. (2001) and Laio, et.al. (2001a), as well as the dynamic stress and the soil moisture transient response for each vegetation type and rooting scenario. In addition, the soil moisture pdf's from actual soil moisture data are calculated for the California blue oak savanna site and compare these to the predictions by the hydrologists' model. Below are presented key points of Rodriguez-Iturbe, et.al.'s (2001) model, the parameterization for a California blue oak savanna, comparisons between predicted and measured soil moisture pdf's, and a discussion the meaning of the vegetation transpirativity and soil moisture stress points with respect to real plant processes. The analysis here adds to the ecohydrological theory by emphasizing the role of variation in energy seasonally in determining maximum plant transpiration. In addition, the results of probabilistic soil moisture model help to define the as yet poorly known bounds on grass and blue oak rooting depths in the Ione

savanna.

3.2 Soil moisture model

Rodriguez-Iturbe, et.al.'s soil moisture balance model (1999) is a hydrologists' standard, one-dimensional point mass conservation model, in a stochastic differential equation:

$$nZ_r ds = dR - dQ - Ldt - E dt \quad (3.1)$$

where:

- n = soil porosity
- Z_r [m] = rooting depth
- ds [dimensionless] = stochastic soil moisture change relative to saturation
- dR [m] = stochastic rainfall input minus interception
- dQ [m] = stochastic run-off loss
- L [m d⁻¹] = deterministic leakage loss rate
- E [m d⁻¹] = soil evaporation rate plus vegetation transpiration rate

Note that soil moisture, s , is normalized relative to saturation, i.e. s is volumetric soil moisture divided by saturated volumetric soil moisture.

Stochastic rainfall-minus-interception is modeled as a marked Poisson process, with probability of a rainfall event being λ_R (mean storm frequency, days⁻¹) and depth of rainfall events being a random variable H . The input from rainfall at time t is:

$$dR = H de \quad (3.2)$$

where H is the depth of rainfall events, an exponential random variable with mean α :

$$f_H(h) = \frac{1}{\alpha} \exp\left(-\frac{1}{\alpha}h\right) \text{ for } h \geq 0 \quad (3.3)$$

and u is the indication of a rainfall event in a marked-Poisson process. To take into account interception by vegetation, λ is simply imposed to be for rain events that are deeper than

a threshold depth of D(LAI). This simply gives a new marked-Poisson process with mean time between events λ' (Laio, et.al., 2001). Note that with additional rigor, it would be desirable to distinguish interception by open tree canopies versus bare soil or open areas, but for now, this parameterization is expedient:

$$\lambda'_R = \lambda_R \int_{\Delta}^{\infty} f_H(h) dh \quad (3.4)$$

This gives the occurrence of rainfall input as:

$$de = \left\{ \begin{array}{l} 1 \text{ with probability } \lambda_R dt + o(dt) \\ 0 \text{ with probability } (1 - \lambda_R) dt + o(dt) \end{array} \right\} \quad (3.5)$$

Note that this classic statistical representation of precipitation requires specification of a time period within which these statistics can be characterized within the marked-Poisson distribution. This then requires distinguishing different seasons for a particular climate.

Run-off, $Q(s, dR)$ [m], is a function dependent on the rainfall rate and the soil moisture, $Q = Q(S, R)$. The run-off is simply the amount of precipitation minus infiltration that is in excess of the amount needed to saturate the soil.

Leakage loss rate, $L(s)$ [cm d⁻¹], is represented as in Laio, et.al. (2001), Equation (14), as a function of soil moisture, $L=L(s)$. Below, their equations are presented verbatim:

$$L(s) = \frac{K_s}{e^{\beta(1-s_{fc})} - 1} \left[e^{\beta(s-s_{fc})} - 1 \right] \quad \text{for } s_{fc} < s \leq 1 \quad (3.6)$$

where:

K_s [cm d⁻¹] = saturated hydraulic conductivity of the soil

s [dimensionless] = relative soil moisture

b = coefficient that fits the above expression to a power law:

$$L(s) = K(s) = K_s s^{2b+3}$$

where:

$K(s)$ [cm d⁻¹] = hydraulic conductivity of the soil

b = parameter in soil-water retention curve, relating soil moisture of a particular soil type to soil water potential

Laio, et.al. (2001) represent evapotranspiration, $E(s)$, as a piecewise function for different soil moisture ranges. According to plant leaf gas exchange studies in the plant ecophysiological literature, many plants exhibit a maximum transpiration rate when they are not water stressed, and then show a linear decline in transpiration relative to soil moisture (Schulze, 1986). Laio, et.al. (2001) therefore define various soil moisture cut-off points (in terms of values relative to saturation when $s = 1$): field capacity, s_{fc} ; onset of water stress, s_* ; wilting point, s_w ; and s_h , hygroscopic point. Their model then has evapotranspiration rate always at its maximum, E_{max} , when vegetation is unstressed, i.e. when soil moisture is above, s_* ; and then evapotranspiration linearly declines down to some minimum level, E_w , at the wilting point, s_w :

$$E(s) = \begin{cases} E_w \frac{s-s_h}{s_w-s_h} & s_h < s \leq s_w \\ E_w + (E_{max} - E_w) \frac{s-s_w}{s_*-s_w} & s_w < s \leq s_* \\ E_{max} & s_* < s \leq 1 \end{cases} \quad (3.7)$$

This representation approximately separates soil evaporation and vegetation transpiration at low soil moisture levels, by also specifying a linear decline in evaporation below the wilting point continuing down to the hygroscopic point. Note that while $s_{saturation}$, s_{fc} , s_h , and E_w are functions of soil texture, the parameters s_* , s_w , and E_{max} are dependent on plant characteristics, which must be known beforehand. These last three parameters are not generally straightforward to quantify.

3.2.1 Probabilistic indicators

From the above soil moisture balance model, Rodriguez-Iturbe, et.al. (1999b) and Laio, et.al. (2001) derived the probability density function(pdf), $p(s)$, for soil moisture, s ,

for given climate, soils, and vegetation. From this pdf, Porporato, et.al. (2001) further derived measures of plant water stress.

A "static water stress" quantifies the immediate stress a plant experiences relative to a soil moisture level between its stress point, s_* , and wilting point, s_w . Since a plant may endure periods of stress and recovery, the researchers were additionally interested in quantifying the "dynamic water stress," the amount of stress a plant is likely to be subject to over a period of time. They derive expressions for the mean number of times the soil moisture level will cross a particular value, as well as the mean time between such crossings. The dynamic water stress, $\bar{\theta}$, is then the ratio between the stress imposed by the system (from the crossing properties relative to s_*) and the amount of stress the particular plant species is able to endure over specified time period.

In the course of deriving these quantities, Porporato, et.al. (2001) introduce two vegetation parameters that are species-specific: a parameter, q_{stress} , to account for the possible non-linearity of the effect of stress on the plant's condition (for static stress); and a parameter, k_{stress} , as a fractional measure of the plant's resistance to drought (in the dynamic water stress). These parameters have no clear physical quantification, but they offer more conceptual completeness to account for variation in plant physiologies; they may serve possibly as fitting parameters when examining a real ecosystem, and further investigations may eventually identify corresponding vegetation drought strategies to scale with q_{stress} or k_{stress} .

In the analyses below, the default parameterizations are used of $q_{stress} = 1$ (linear relation of stress to plant condition) and $k_{stress} = 0.5$, a vaguely chosen middle value (sensi-

tivity analyses are given in Porporato, et.al., 2001). The soil moisture pdf's are calculated, $p(s)$, and the dynamic water stress, $\bar{\theta}$. For the dynamic water stress, the calculation here departs slightly from the original researchers' calculation. They used an expression for mean static water stress *conditional* on the plant experiencing stress (Equations 17 and 28 in Porporato, et.al., 2001). However, as the seasons of interest for the blue oak savanna span times both with and without water stress, just the mean static water stress is used (Equation 16 inserted into Equation 28 in Porporato, et.al., 2001) without conditioning on the state of the vegetation in order to intercompare seasons. The reader may refer to Appendix I for the fairly complicated expressions of Laio, et.al. (2001a) and Porporato, et.al., (2001).

3.3 Study site

The site of interest is a California blue oak (*Quercus douglasii*) savanna with annual grasses in Ione, California, in the low foothills of the Sierra Nevada (38° 26' N, 120° 57' 30" W, elevation ~175 m). The climate is Mediterranean and semi-arid, with winter rain and summer drought. Mean annual precipitation is 610 mm, and mean annual temperature is 16° C (mean maximum 40° C, mean minimum 5° C). Soils are a rocky loam (Auburn series, sand/silt/clay percentages 38/45/18 under tree canopies and 48/42/10 in open grass areas), on 0.5-1.0 meter deep above greenstone bedrock (bulk density 1.42 g cm⁻³ under the trees, 1.52 g m⁻³ in the open). Groundwater sources occur at 200 m and 340 m depths (Russell Tonzi, personal communication). The site is level, with maximum slopes in undulations of less than 15%.

Vegetation at the site is comprised of an scattered canopy of blue oak trees and a small number of grey pines (*Pinus sabiniana*) over an herbaceous understory. The annual grass and herbaceous layer is active during the wet winter to early spring, and the drought-deciduous blue oaks leaf out a 1-2 months before the grasses senesce and are active through the end of the summer. The density of the blue oaks is approximately 200 trees per hectare, with canopy cover of 0.39, and peak leaf area of 0.6. The very minor population of grey pines has a variable density of 3-24 per hectare. The site is lightly grazed during the early spring, and the owner manages the vegetation to exclude shrubs.

Measurements of evapotranspiration and micrometeorological variables have been conducted continuously at the site starting in late 2000 for the open grass areas and starting in early 2001 for the tree canopy and tree-covery understory (Kiang, et.al., this dissertation). Here, soil moisture and evapotranspiration data from 2001 are used.

3.3.1 Climate statistics

Climate parameters were generated for the marked-Poisson distribution by summarizing 10 years of precipitation data from California Department of Water Resources, Station Ben Bolt (38° 35' N, 121° 1' W, elevation 347 m). This weather station is located 25 miles north of Ione with the same type of vegetation and precipitation regime as that at Ione (Rich Green, Unit Chief, Amador-El Dorado Unit, California Department of Forestry, personal communication). The times series of precipitation, time between storms, and storm depth show a clear seasonality in precipitation, as shown in Figure 3.1.

To check the distributions for the marked-Poisson process, the mean storm arrival rate, λ_R , and the mean rainfall depth, α , were calculated for each month to assess seasonal

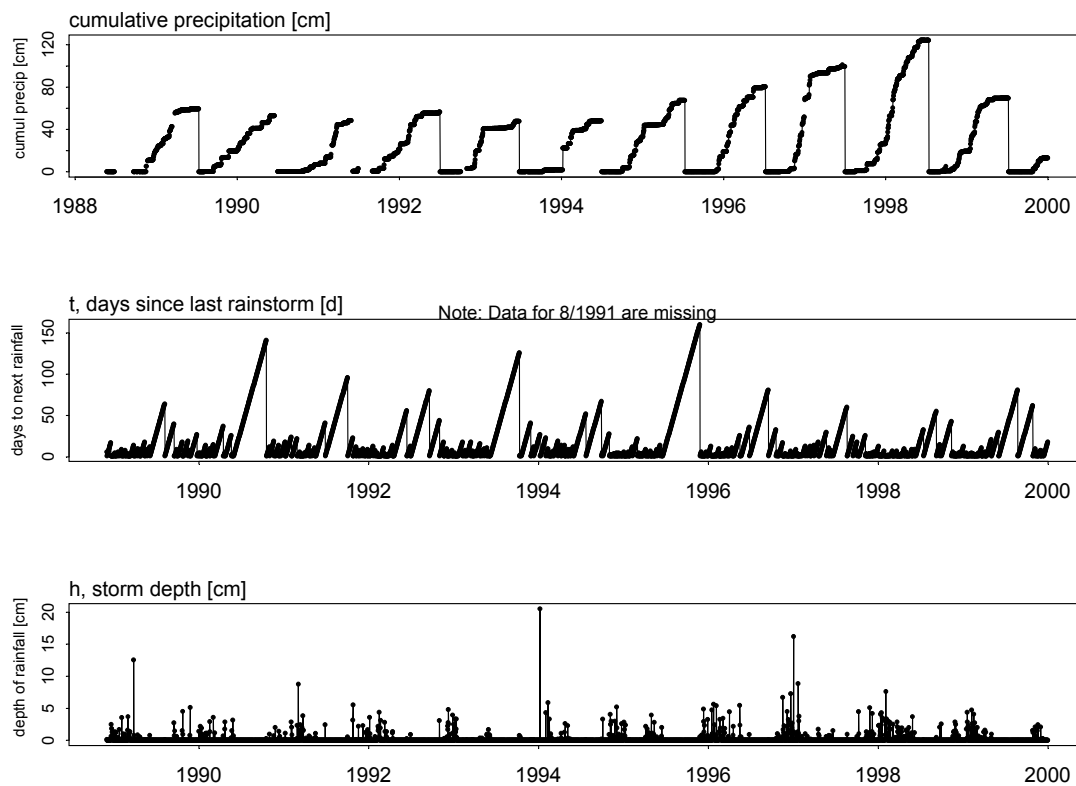


Figure 3.1: Precipitation in Amador County, California. Top: cumulative precipitation. Middle: days between storm events. Bottom: storm depth [cm]. (California Department of Water Resource, Station Ben Bolt, 1988-1999).

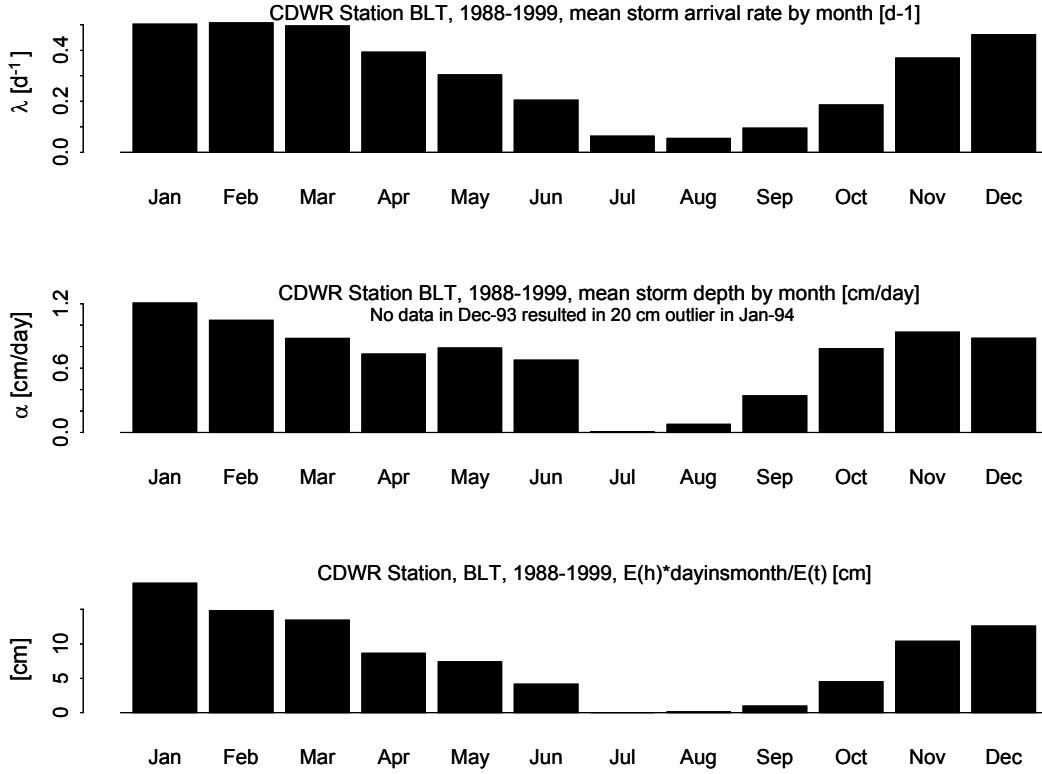


Figure 3.2: Monthly parameters for marked-Poisson characterization of precipitation in Amador County, California. Top: storm arrival rate, λ_R [d⁻¹]. Middle: mean storm depth, α [cm]. Bottom: approximate mean monthly precipitation. (California Department of Water Resource, Station Ben Bolt, 1988-1999).

periods when these parameters are approximately constant, shown in Figure 3.2. The bottom chart in the figure gives an estimation of mean monthly precipitation, showing a clearly dry summer.

Given these statistical distributions, three different seasons were specified as having distinct precipitation patterns: a winter wet season (November-February), a spring early dry season of initial soil moisture dry-down (March-June), and a late summer dry season (July-October). Since the growing periods for the grasses and oaks each span two

Season	λ_R [d ⁻¹]	α [cm]
Winter (Nov.-Feb.)	0.461	1.017
Spring (Mar.-Jun.)	0.349	0.768
Summer (Jul.-Oct.)	0.100	0.302
Grass growing season (Nov.-Apr.)	0.455	0.946
Oak growing season (Mar.-Oct.)	0.224	0.535

Table 3.1: Seasonal storm frequency and mean storm depths for Ione, CA (California Department of Water Resources)

seasons, the precipitation parameters were calculated for these periods as well. The storm frequencies, λ_R , and mean storm depths, α , are given in Table 3.1. The histograms of the storm arrival times and storm depths are given by season in Appendix H to show their respective distributions.

3.3.2 Vegetation rooting depth

Rooting depth was not directly sampled at the Ione savanna site, so data from the literature were relied on for values of the parameter Z_r for the trees and the grasses.

According to previous studies (Griffin, 1973), and given the drought-deciduous nature of blue oaks (Muick and Bartolome, 1987), it is believed that blue oak trees do not access deep water sources below the soil layer. On the other hand, hydraulic lift has been observed in blue oaks (Ishikawa and Bledsoe, 2000). It is unclear how deep the source of hydraulically lifted water could be. Direct data on blue oak rooting distribution are few and recent. At a more mesic, higher elevation site (70 cm mean annual precipitation) than Ione, Millikin and Bledsoe (1999) found blue oak rooting depth to range from 0.5 to 1.5 m, with about 70% of the root biomass located above 0.5 m. At the same site, Cheng and Bledsoe (2002) sampled oak fine roots in 40 cm-deep ingrowth cores, and found strong

seasonal variation in production, with negligible fine root production in the fall and winter, and peak production in spring and summer. In the spring, the depth distribution of blue oak fine roots is approximately uniform, while in the summer, there is a strong decline in the shallow blue oak fine roots above 20 cm and increase in production below 20 cm.

Cheng and Bledsoe (2002) observed annual grass root production in 40 cm-deep ingrowth cores. Production peaked in fall and winter, with the bulk of fine roots in the upper 0-20 cm; in the spring, the grass fine roots shifted to even depth distribution but very low production throughout the measured 0-40 cm depth, with full senescence in the middle of this period. The peak growing season dominant production in the upper 20 cm is the same as observed by Jackson, et.al.(1988).

From these studies, it seems that the blue oaks at the Ione site do not tap the deep groundwater, but their roots remain in the 0.5-1.0 m soil layer above rock, but more confirmation is necessary. From the study of Millikan and Bledsoe (1999), the oaks and grasses appear to favor different soil depths for soil moisture when their growth is out-of-phase (winter grass, summer oaks), but their root depth distributions are the same when their growth is in phase (spring). However, during the spring, the grasses are already senescing, such that their root density is declining, and there seems to be little time for competition between the oaks and grasses for soil moisture. Therefore, the grass root depth may be considered predominantly shallower than that of the oaks. The possibility of hydraulic lift complicates the definition of what depth of soil moisture is accessed.

For the ecohydrological model, the oak and grass root depths are parameterized in two different schemes. The first scheme considers that the entire 100 cm soil profile

is available to both functional types, using the rationale that both the grass and oak roots are able to penetrate to the bottom of the soil despite uneven depth distributions (soil pit excavation at the Ione savanna site, and Millikin and Bledsoe, 1999), and that hydraulic lift by the oaks provides the grasses indirect access to the deeper soil moisture (Ishikawa and Bledsoe, 2000). The second scheme follows the root depth profiles as found in the literature: grass root density concentrates most in the upper 20 cm, and 70% of oak root density concentrates in the upper 50 cm, so the total significant oak root depth is parameterized to 60 cm. The two different scenarios are compared with respect to their values for dynamic stress and their ability to mimic actual observed soil moisture.

3.3.3 Vegetation evapotranspiration and interception

For values of E_{max} and E_w for the grasses and oaks, the maximum and minimum fluxes as measured by eddy flux at the Ione site were used (Baldocchi, et.al., in preparation; Kiang, this dissertation). Laio, et.al. (2001) also use maximum measured (lysimeter) transpiration values. This characterization of vegetation "transpirativity" is not deeply scrutinized by Rodriguez-Iturbe and co-workers, and will become a point of discussion later, as obviously the weather conditions influence what fluxes can be observed. Because the grasses experienced reduced transpiration in the winter despite abundant soil moisture (Kiang, this dissertation) and higher transpiration in the spring, different values of E_{max} were used for the winter and spring in separate seasonal calculations of $p(s)$. For the oaks, just the maximum transpiration level observed during the spring were used, since energy is not limiting transpiration during their spring-summer growth period. For E_w , the minimum observed flux during the late summer as measured by eddy flux at the Ione site was used.

	$Z_r(1)$	$Z_r(2)$	s_w	s^*	$E_{\max}$
	cm	cm	vol vol ⁻¹		cm d ⁻¹
grass	100	20	0.27	0.65	0.25 winter 0.40 spring
blue oak	100	60	0.22	0.45	0.25

Table 3.2: Ione soil characteristics and plant-soil moisture critical parameters. $Z_r(1)$: root depths spanning soil depth; $Z_r(2)$: root depths following observed root density distributions.

For rainfall interception by vegetation, since the Ione savanna site has very similar canopy cover to that at Nylsvely, South Africa, on which Laio, et.al. (2001b) tested their stochastic model, their same values of $\Delta_{grass} = 0.1$ cm and $\Delta_{oaks} = 0.2$ cm were used here.

The model parameterizations for vegetation are summarized in Table 3.2. The critical soil moisture points for vegetation are described in the next section on soil moisture parameters.

3.3.4 Soil moisture parameters

Normalized soil moisture, s , is calculated relative to saturated soil having $s = 1$, as in Laio, et.al. (2001a):

$$s = \frac{\theta_{soil}}{\theta_{sat}} \quad (3.8)$$

where θ_{soil} [volume water / volume soil] is volumetric soil water content, and θ_{sat} [volume water / volume soil] is the soil water content at saturation (equal to the porosity). When discussing soil moisture data from the Ione site, depth-weighted (vertical) and canopy cover (horizontal) weighted averages of soil moisture measurements were used (Kiang, et.al., in preparation).

To identify the soil moisture critical points, s_{fc} , s_* , s_w , and s_h , a combination was used of observed soil moisture values and soil water potential relations (plant physiological

relations; soil moisture release curves; model of Saxton, et.al., 1986). The following empirical relation from Ione soil measurements was used to interconvert between relative soil moisture and soil water potential (Xu, unpublished):

$$\Psi[MPa] = -0.00483 s^{-2.5656} \quad (3.9)$$

Field capacity, s_{fc} , of the Ione site's soil was estimated by comparing soil texture-moisture relations developed by Saxton, et.al. (1986) and soil moisture data during the wet season. Saxton's prediction of field capacity of 0.67 (volumetric 0.26) is a low estimate, since it does not account for the presence of organic matter, which will raise the field capacity of a soil. Observations at the site showed a higher field capacity around 0.80 (volumetric 0.31), and therefore this value was used for the stochastic model

The hygroscopic point, s_h , is responsible for a negligible amount of water compared to that utilized by the plants, and also, hygroscopic water is a somewhat imprecise quantity dependent on atmospheric conditions: it is variously defined as water held within 0.0002 mm of soil particle surfaces (Pidwirny, 2000); water adsorbed to dry soil at high relative humidity, or water lost from air-dry soil heated to 105 C; or water held by soil at equilibrium with an atmosphere at 98% relative humidity and 25 C (Agriculture and Agri-Food Canada). Since hygroscopic water is a comparatively negligible quantity that is not important for the temporal dynamics of the soil moisture, the practice of Laio, et.al. (2001b) is followed, specifying s_h to be within a correct order of magnitude, equal to the soil moisture when soil water potential is -10 MPa, $s_h = 0.05$.

For vegetation stress points, s_* and s_w , a combination of indicators and measurements were used: plant-soil water potential relations from the plant physiological literature,

eddy flux data, and leaf twig water potential data (Kiang, et.al., this dissertation). For the grasses, it was observed when the grass transpiration eddy flux data began to decline with soil moisture and set $s_{*,grass}$ to the soil moisture at this time, $s_{*,grass} = 0.65$. For grass wilting point, $s_{w,grass}$ the common wilting point for plants was used, which occurs when soil water potential is about -1.5 MPa (Nobel, 1999), or $s_{w,grass} = 0.27$.

Because blue oaks have drought-tolerant strategies (Muick and Bartolome, 1987), their wilting point can be far lower than -1.5 MPa, as low as -4.5 MPa xylem water potential (Griffin, 1973; measurements at the Ione site in Kiang, et.al., in preparation), which is similar to plants in other semi-arid environments (Laio, et.al. 2001a; Larcher, 1995; Scholes and Archer, 1993). The concurrent soil moisture observed at the Ione savanna site were slightly higher than the leaf twig water potential -4.5 MPa, and therefore the wilting point was specified at the observed value, $s_{w,oak} = 0.22$ (equivalent soil water potential of -2.6). For $s_{*,oak}$, the analysis of Kiang, et.al. (this dissertation) was used, which determined the onset of stress by advanced regression of tree transpiration versus several driving variables, including relative soil water content. After converting their value for relative extractable water (REW) to equivalent normalized soil moisture, the value obtained for $s_{*,oak}$ is 0.45.

For soil hydraulic conductivity, the relation in Saxton, et.al. (1986) for loam soils was used, calculating a canopy cover area-weighted average to obtain $K_s = 50 \text{ cm d}^{-1}$.

The soil characteristics and critical moisture points for parameterizing the ecohydrological model are summarized in Table 3.3.

soil type	n	depth	K_s	s_h	s_{fc}
	vol vol ⁻¹	cm	cm d ⁻¹	vol vol ⁻¹	
Ione loam	0.39	100	50	0.05	0.80

Table 3.3: Soil physical characteristics at the Ione, CA, savanna.

3.3.5 Observed soil moisture probability density distributions

To compare the stochastic model predictions of soil moisture distributions with observation, simple binning was performed of observed, half-hourly soil moisture data. Data gaps were filled with line interpolation, as the time scale of soil moisture change is not generally significant below the daily time scale.

3.4 Results

The time course of soil moisture measured at the Ione site in 2001 is shown in Figure 3.3. Soil moisture hovers around field capacity during the winter, then steeply declines in the spring with the end of the winter rains, converging to a minimum value for most of the summer.

Figure 3.4 shows 2001 trends in evapotranspiration broken down by open grass areas, tree-covered understory, trees only, and total ecosystem fluxes above the overstory. Since the grass and soil fluxes are measured by eddy flux, their evapotranspiration is combined. Grass and soil evapotranspiration in open areas (Figure 3.4) is low during the wet winter, rising quickly in the spring, and then dropping dramatically with soil moisture drying at the end of spring, with grass senescence before the summer. Tree-covered understory fluxes follow the same pattern, but moderated in magnitude by the tree canopy shading.

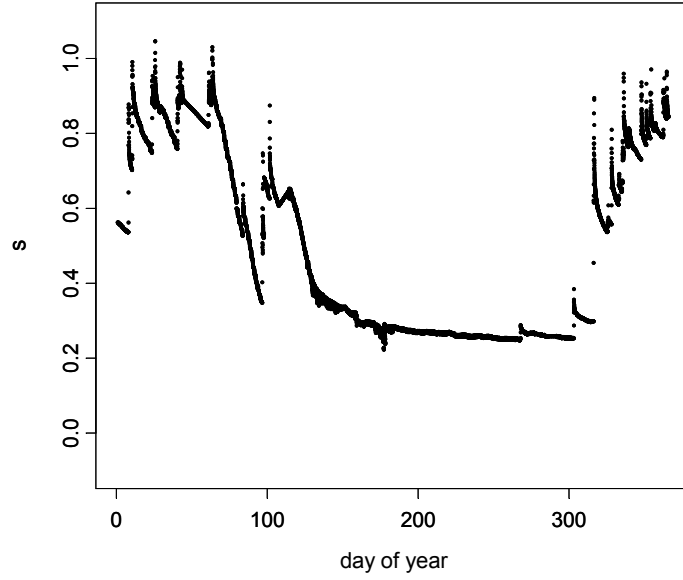


Figure 3.3: Normalized soil moisture trends for 2001, Ione, CA, savanna site.

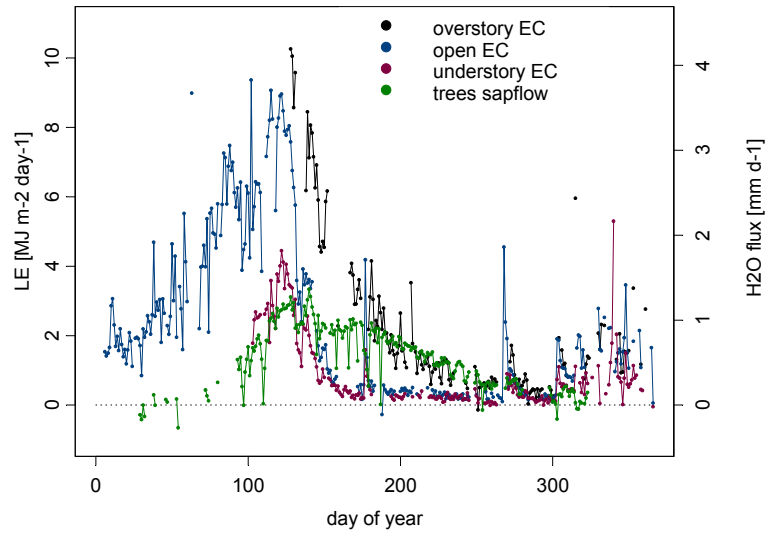


Figure 3.4: Evapotranspiration as measured by eddy covariance (EC) and sap flow techniques for 2001, Ione, California, savanna site (Kiang, this dissertation).

Tree transpiration begins with leaf-out in the early spring (March 21, Day 80), reaching a brief peak, and then declining at a remarkably linear rate over the course of the summer, despite the rapid rate of soil dry-down.

The soil moisture pdf's, both predicted and observed, for the full growing seasons of the grass and oak layers in Ione are shown in Figure 3.5 for the parameterization of oak and grass rooting depths as 100 cm, and in Figure 3.6 for oak rooting depth of 60 cm and grass depth of 20 cm.

The predicted pdf for the dominant tree species, *Burkea africana*, in the savanna in Nylsvley, South Africa, is also included to compare to Rodriguez-Iturbe and co-workers' application of the model (data from Scholes and Walker, 1993). The latter site receives the same amount of annual precipitation as the Ione savanna, but the rainfall is distributed throughout the warm growing season; also, the soils at Nylsvley are sandy, in contrast to loam at Ione. The pdf's clearly show the overall wetter growing season of the grasses compared to the oaks, and the lower soil moisture available in the sandy soil at Nylsvley. For the two different rooting depth scenarios – the full soil profile versus the root density distributions – the latter case produces a clearly better approximation to the 2001 soil moisture data for the oaks, but it is not clear which is more realistic for the grasses, due to the somewhat multi-modal pattern of the data.

To understand the vegetation condition during these growing periods, it is necessary to examine the relation of the soil moisture pdf's to the vegetation stress points (as the soil moisture values are not alone adequate indicators, since water potential is the actual quantity to which plants physiologically respond). The dynamic stress calculated from

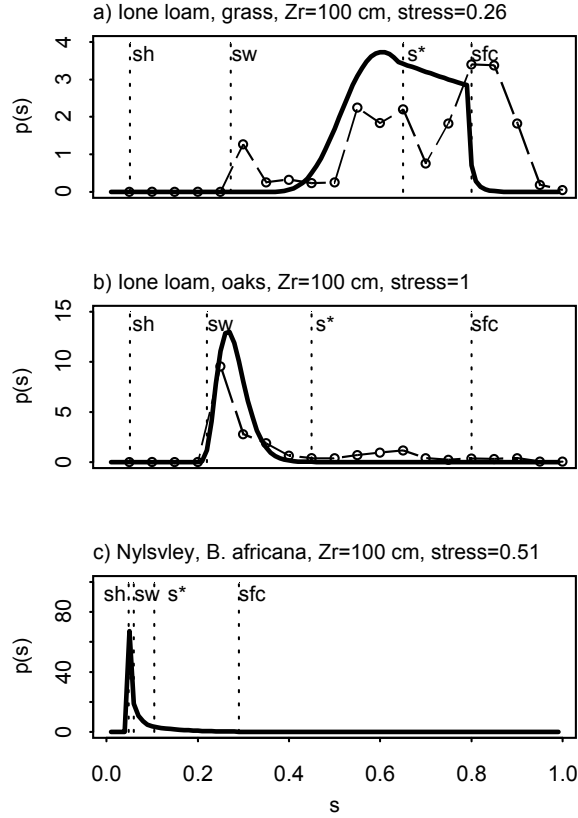


Figure 3.5: Probability density functions (pdf's) of soil moisture (bold lines) for both grass and blue oak rooting depths of 100 cm. Pdf's predicted by stochastic model of Rodriguez-Iturbe and co-workers, with observations from an Ione, California, savanna (dashed lines with markers). Z_r is rooting depth. Stress is the dynamic stress, θ . s_{fc} , s_* , s_w , and s_h mark the soil moisture critical points as defined in the text. a) Ione, grass full growing season (Nov.-Apr.). b) Ione, oak full growing period (Mar.-Oct.). c) Nylsvley, South Africa, *Burkea africana* tree.

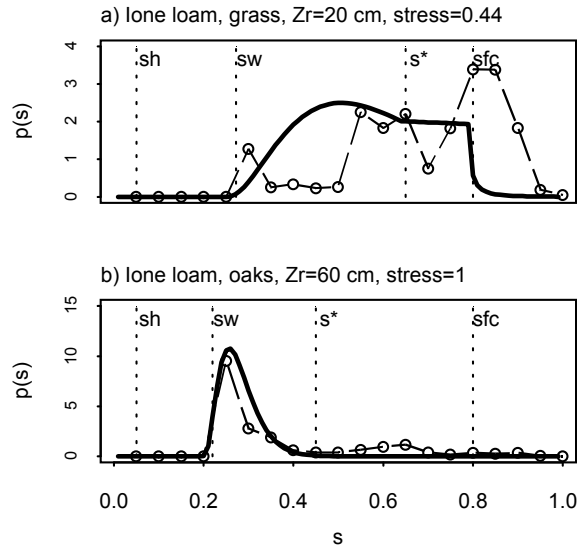


Figure 3.6: Probability density functions (pdf's) of soil moisture (bold lines) for both grass and blue oak rooting depths of 20 cm and 60 cm, respectively. Pdf's predicted by stochastic model of Rodriguez-Iturbe and co-workers, with observations from an Ione, California, savanna (dashed lines with markers). Z_r is rooting depth. Stress is the dynamic stress, θ . s_{fc} , s_* , s_w , and s_h mark the soil moisture critical points as defined in the text. a) Ione, grass full growing season (Nov.-Apr.). b): Ione, oak full growing period (Mar.-Oct.). c): Nylsvley, South Africa, *Burkea africana* tree.

these periods is a low 0.26 (root depth 100 cm) and 0.44 (root depth 20 cm) for the grasses, the highest 1.00 for the oaks, and a middle value of 0.51 for the trees at Nylsvley. Shallower root depth implies higher overall dynamic stress for the grasses. From these calculations, it would appear that the oaks are always severely stressed and that grasses should dominate at the Ione savanna, while the Nylsvley trees experience a more even distribution of soil moisture ranges relative to their stress points. However, if the soil moisture pdf's and dynamic stress values are examined by season rather than full growing period, it becomes clear why the grasses and oaks trade off in growth in the spring at Ione.

The probability density functions of soil moisture by season and vegetation type for Ione climate are shown in Figure 3.7 for the 100 cm root depth scenario and in Figure 3.8 for 20 cm grass root depth, and 60 cm oak root depth (grass winter, grass spring, blue oak spring, blue oak summer). The dynamic water stresses for both these seasonal breakdowns and the full growing periods and for both rooting depth scenarios are plotted in Figure 3.9.

Both model and data show the distinct seasonal differences in soil moisture distribution, from the wet winter during which the grasses experience virtually no stress; to the spring when grasses are almost entirely in their stressed soil moisture ranges while the oaks straddle unstressed and stressed regions; and the summer when the oaks straddle their wilting point. The seasonal breakdown explains why the grasses decline in the spring while the oaks take over, because the oaks experience an overall lower dynamic stress than the grasses during this transitional season. The high stress of the oaks during the summer corresponds to their gradual senescence in response to drought during this period.

Why the dynamic stress of the grasses should be lower in the spring for the shal-

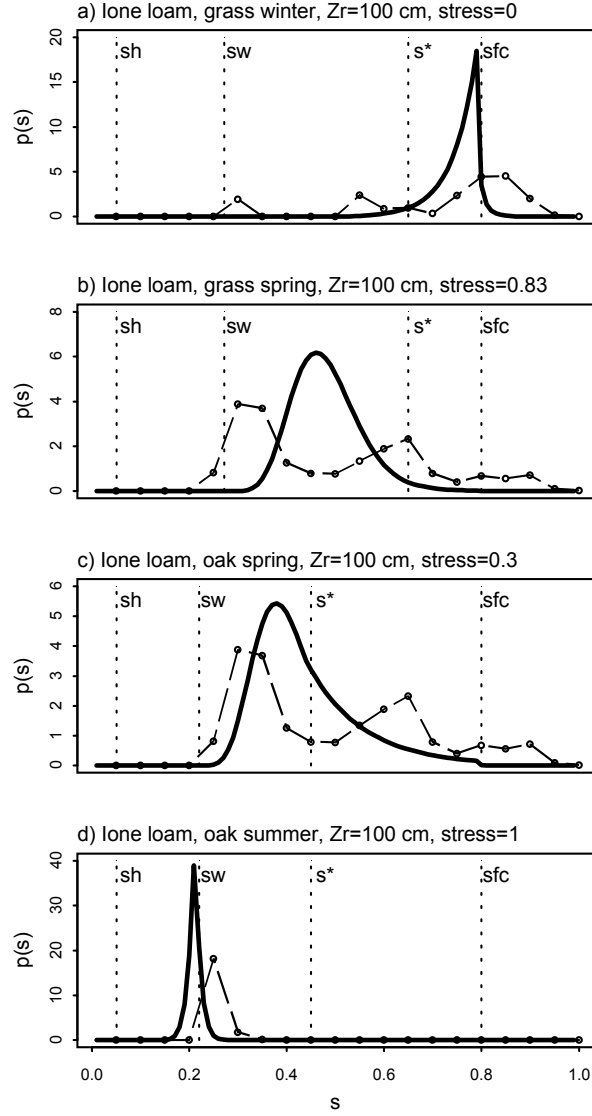


Figure 3.7: Probability density functions of soil moisture (bold lines) for grass and oak root depths of 100 cm. Pdf's predicted by stochastic model of Rodriguez-Iturbe and co-workers, with observations from an Ione oak savanna site (dashed lines with markers). Z_r is rooting depth. Stress is dynamic stress, θ . s_{fc} , s^* , s_w , and s_h mark the soil moisture critical points as defined in the text. a) grass, winter (Nov.-Feb.). b) grass, spring (Mar.-Jun.). c) oak, spring (Mar.-Jun.). d) oak, summer (Jul.-Oct.).

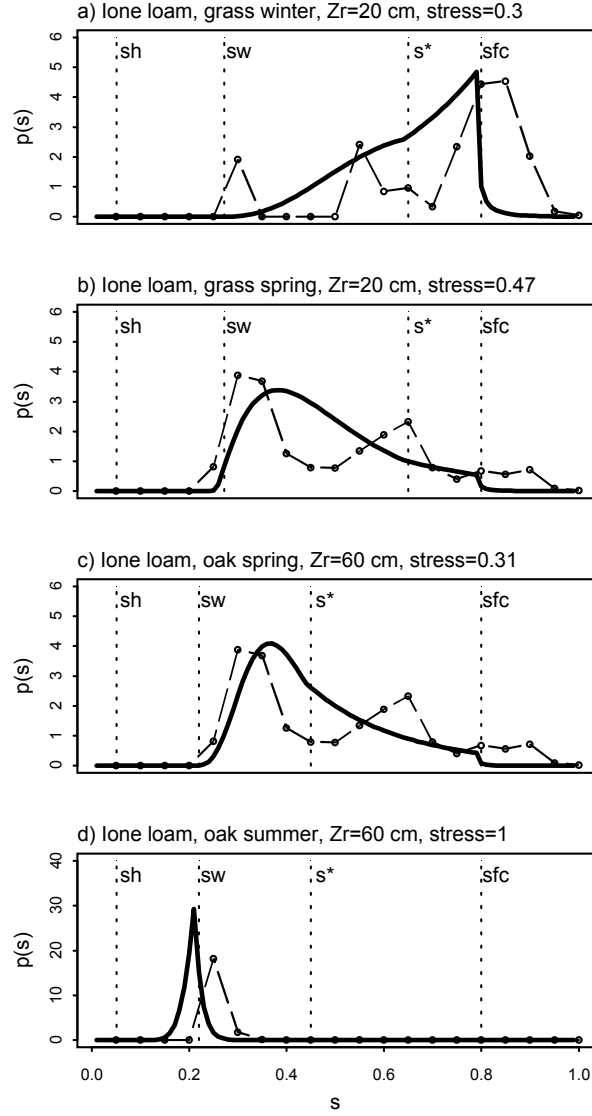


Figure 3.8: Probability density functions of soil moisture (bold lines) for grass and oak root depths of 20 and 60 cm, respectively. Pdf's predicted by stochastic model of Rodriguez-Iturbe and co-workers, with observations from an Ione oak savanna site (dashed lines with markers). Z_r is rooting depth. Stress is dynamic stress, θ . s_{fc} , s^* , s_w , and s_h mark the soil moisture critical points as defined in the text. a) grass, winter (Nov.-Feb.). b) grass, spring (Mar.-Jun.). c) oak, spring (Mar.-Jun.). d) oak, summer (Jul.-Oct.).

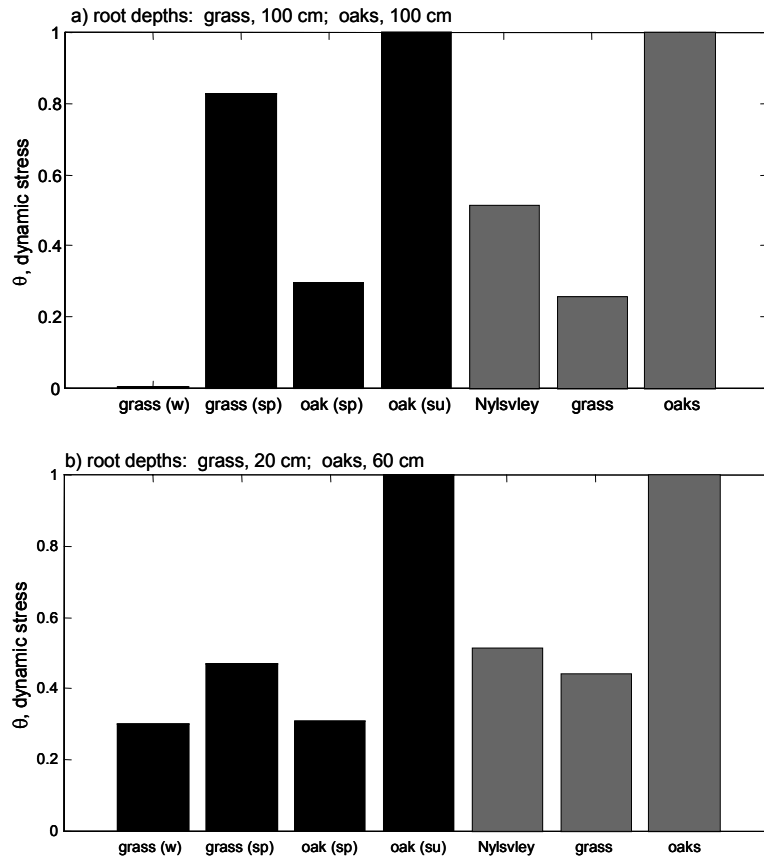


Figure 3.9: Predicted dynamic water stress by season (black: w-winter, sp-spring, su-summer) and by total growth period (grey) of grass and blue oak trees in Ione, California, and of *Burkea africana* in Nylsvley, South Africa. a) root depths Z_r of 100 cm for both grass and oaks; b) root depths Z_r of 20 cm for grass and 60 cm for oaks.

lower rooting depth (dynamic stress 0.47) than for the deeper parameterization (dynamic stress 0.83) provokes some questions. The predicted soil moisture pdf for oaks in the spring is less skewed into the stressed soil moisture region with the 60 cm root depth than with the 100 cm root depth. That is, the soil moisture is more evenly distributed across a wide range of values, such that, over time, the blue oaks could experience an overall lower dynamic stress with a shallower root depth. The explanation must be that the precipitation at this site is too low to saturate through always to the deep soil, such that soil moisture restricted to the shallow soil then implies a higher REW than if the REW had been calculated through to depths to which the precipitation does not percolate. Under such dry conditions where rain is the only source of water and there are no deep ground sources, the vegetation gains no benefit from rooting deeper. Thus, this hydrologists' model can help constrain root depths based on the soil moisture balance.

The predictions by the stochastic model of Rodriguez-Iturbe and co-workers reproduce the 2001 soil moisture distributions most closely for the rooting density distributions as observed by Millikan and Bledsoe (1999), where grasses are shallow rooted at 20 cm, and oaks access mostly down to 60 cm. This theoretical prediction thus provides firmer evidence that the rooting depths of the two functional types are indeed different. This theoretical match could imply there is minimal access to deeper soil moisture and that hydraulic lift may be negligible. On the other, that the dry year 2001's observed soil moisture pdf's are under-predicted in the winter/grass season as well as the summer/oak season implies either that the soil parameterization for field capacity and hygroscopic point are too low, or that the observed REW was inaccurately measured, or that the vegetation are accessing

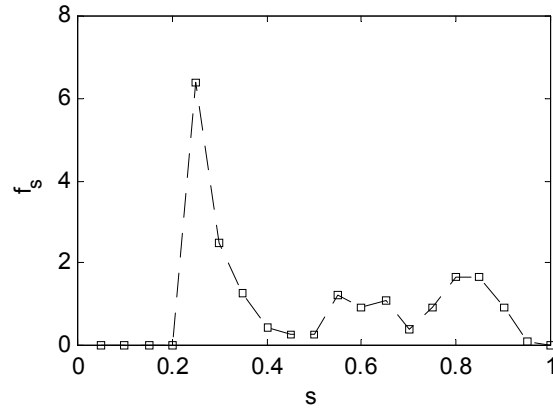


Figure 3.10: Frequency distribution of observed soil moisture for the entire year 2001 at Ione savanna site, California.

some other soil moisture. More about the match between the model and 2001 data will be discussed later in the Discussion section. Deviations between the observed and predicted values could be due to measurement errors, imprecision in identification of stress points for the vegetation, the choice of seasonal cut-off points which might not be strictly the same every year, and the fact that the year 2001 was drier than normal. In particular, the saddle in the observed values for the spring in Figures 3.7 and 3.8 is most likely due to the choice of seasonal cut-off points in binning data when there is interannual variation. The only way to solidly verify the match between the theory and actual root depths, of course, would be to collect several years of soil moisture data to analyze their mean behaviors. The distribution of observed soil moisture through the whole year (Figure 3.10) shows a distinct trimodal distribution that seems to correspond to the winter, spring, and summer seasons. The stress point for oaks, $s_{*,oaks} = 0.45$ appears to correspond to the transitional point between spring and summer soil moisture distributions (the valley in the curve at $s = 0.45$

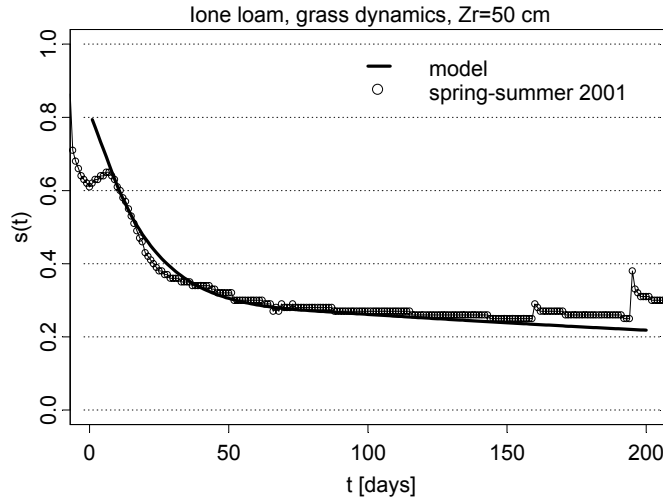


Figure 3.11: Probabilistic transient dynamics of soil moisture for grass as predicted by model of Rodriguez-Iturbe (2000), shown with actual soil moisture data from the Ione savanna site, spring-summer 2001. Data are a depth-weighted average from measurements down to 50 cm.

in Figure 3.10).

Considering that 2001 was a drier year than normal, it would be expected that the stochastic model would predict greater overall soil moisture, compared to the dry year. Since there would be year-to-year variation in observed soil moisture pdf's, more years of data would be needed to confirm how well the statical pdf fits the means of several years. Another assessment of model performance can be done by examining the soil moisture transient responses, seeing how well the model and data match in the time course of dry-down from some starting value of soil moisture. The course of dry-down should be the same for an initial given soil moisture values regardless of season. These transient dynamics are shown in Figure 3.11. Since the soil moisture probes provided a profile only down to 50 cm, the transient dynamics shown here are for an equivalent grass root depth of 50 cm. The

depth-weighted soil moisture data and predicted response are plotted so as to intersect at a mutual upper value of soil moisture, so that their simultaneous transience may be compared. The actual data appear to exhibit a slightly steeper initial decline than predicted; this may be because the model does not account for simultaneous water uptake by both trees and grasses, a detail that can be easily fixed. Overall, the predicted transient response seems to match the data quite well, departing in the fall only due to the onset of fall rains later in the time series.

3.5 Discussion

The description of the ecohydrology of an ecosystem in terms of its soil moisture probability density distributions and the vegetation's dynamic stress yields clearly-defined seasonal patterns, with observations supporting fairly closely the predictions of the Rodriguez-Iturbe stochastic model. The stochastic quantities provide meaningful indicators of why the different vegetation types have different seasonality. It is encouraging that the predicted soil moisture pdf's corresponded to observations best for rooting depth parameterizations that match the root studies of Millikan and Bledsoe (1999), providing some hope for a theory for predicting root depths when soil moisture measurements but not root excavations can be performed. What is the meaning of these predictions?

That the soil moisture predicted pdf's with shallower rooting depth parameterizations seem to fit the observed pdf's in 2001 might first lead one to conclude that the model supports the observed shallow root depths, implying that the vegetation do not access deeper soil moisture. However, the 2001 data are from a dry year, with 340 mm of precipitation in

the November 2000-October 2001 rain year (California Irrigation Management Information System, Station 131, Fair Oaks, Sacramento), compared to the mean annual level of 610 mm. Therefore, that the observed soil moisture pdf's with shallow root depths match the statistical pdf's, rather than being lower than the statistical distribution, implies that the vegetation in a dry year are somehow getting more moisture than they otherwise should be, given their root depths. This would support the possibility of hydraulic lift enhancing access to soil moisture.

The model of Rodriguez-Iturbe is good for asking the question, given soil, vegetation, and climate characteristics, what is the probabilistic soil moisture distribution, and can we explain the vegetation mix based on their expected dynamic stress? Rodriguez-Iturbe and co-workers have made the important contribution of introducing a parameterization of vegetation stress as influencing evapotranspiration in an ecohydrological model. However, their model relies on an important simplification about vegetation activity. The transpirativity parameter, $E_{\max}$, is not solely a vegetation parameter: it characterizes not just the vegetation but also the energy that is available to drive transpiration. As Rodriguez-Iturbe and co-workers characterize climate only in terms of precipitation, the role of energy still must enter somewhere in order for the model to work. Energy enters through $E_{\max}$ (and also, less significantly, in E_w).

In the case of the Ione savanna, the lack of distinction between seasons can lead to erroneous conclusions about the relative stress levels of the grasses and trees. Low available energy, not drought, in the winter constrains the evapotranspiration of the grass and soil layer, in contrast to the high available energy in the spring, requiring different values for

$E_{\max}$ for grass between these seasons. Salvucci (2001) distinguished seasonal soil moisture pdf's for an Illinois prairie but was interested more in soil properties than in above-ground vegetation features. Here, it is emphasized that energy in the form of transpiration activity is important to account for the soil moisture balance.

Although the stochastic model can distinguish stress levels during the spring, it cannot explain why the trees do not share the winter growing season with the grasses, since there is otherwise abundant water. Again, available energy is required to explain the different functionalities: cold temperatures in the winter can cause embolisms in the oak xylem (Tyree and Cochard, 1996), hindering transpiration, and cold may also limit photosynthetic activity, preventing growth (Woodward, 1987).

In addition to available energy, productivity is a feature implicit in $E_{\max}$ in that it incorporates the leaf area or cover that are available for transpiration. For a soil-vegetation-climate ecohydrological theory, it is desirable that productivity and transpiration be predicted rather than being prior known quantities.

3.6 Conclusions

Climate is a function of both energy and precipitation. Mediterranean ecosystems demonstrate the importance of seasonal distinctions based on the timing of energy and precipitation and not just of plant growing period when formulating an ecohydrological soil moisture balance model. Although water balance indicators that combine measures of available energy and water are nothing new (e.g. Stephenson, 1990, 1998), it is interesting that hydrologists like Eagleson and Rodriguez-Iturbe and co-workers did not attempt ex-

plicitly to account for the role and timing of energy in their models. Both of their models are applicable to systems where available energy is always equal to or greater than the water supply, which is an acceptable restriction when addressing only arid and semi-arid ecosystems. Eagleson's work is primarily useful as a theoretical exploration of long-term equilibrium ideas, while Rodriguez-Iturbe's model works where the water and available energy are in phase. Mediterranean ecosystems challenge ecohydrology to explicitly address the seasonal timing of energy and precipitation, and the importance of this timing in accounting for vegetation productivity and transpiration and the soil moisture balance.

Part II

Optimality of water use at leaf and landscape scales

Summary: Past models of stomatal conductance of plants, and the various attempts to modify them to account for drought, are reviewed. The models are differentiated as those that are empirical, semi-mechanistic, and based on optimality principles. Their abilities to capture various known stomatal behaviors are discussed. The shortcomings of the optimality models are discussed with respect to definitions of “available water” and “optimal.” A new optimality model that incorporates current knowledge about photosynthesis and a clearer accounting of “available water” and “optimal” is developed. The existence of drought results in a model that necessarily accounts for both short-term and evolved plant behaviors, and links leaf and landscape spatial scales. This optimality model shows that the temporal course of stomatal conductance, leaf photosynthetic capacity, landscape leaf area

Stomata of plant leaves must coordinate the uptake of CO_2 on the one hand, and the loss of H_2O vapor on the other; therefore, any model of stomatal control must explicitly treat the drivers of both photosynthesis and transpiration. The state-of-the-art today in semi-mechanistic modeling of stomatal control is combines the Farquhar and von Caemmerer (1982) model of photosynthesis, which models biochemistry within the leaf through Michaelis-Menten descriptions, and the Ball-Berry model of stomatal conductance (1988), which empirically models a fairly consistently observed interaction between assimilation and relative humidity. This combination is called “semi-mechanistic,” since the individual models are in fact empirical, but they explicitly describe the interactions between the driving variables in relations that appear valid across vegetation types. This combination does not require “tuning” (except to input the appropriate, measureable parameters), and

has afforded excellent replication of gas exchange measurements in non-drought conditions (Sellers, et.al., 1996a, 1996b; Baldocchi and Meyers, 1998; Medlyn, et.al., 2001).

The challenge now is to understand how drought causes departure from the Farquhar-von Caemmerer/Ball-Berry representation of stomatal conductance. Plant physiological responses to drought were reviewed in the Chapter 1. To understand how an optimality model for stomatal conductance can be formulated, a review is first provided of the history of stomatal conductance models, from the early empirical, to the details of the semi-mechanistic, to the development of optimality modeling. Discussion is then provided of the shortcomings of current optimality models and how to address them. Finally, the biophysics and biochemistry of stomatal conductance are re-stated in a clear manner, the optimality criteria are formulated, and the links are pointed out between disciplines and between temporal and spatial scales that are necessary in order to fully specify plant optimal stomatal control.

Chapter 4

The vegetation-climate connection

4.1 Landscape scale:

theories of climatologists and hydrologists

That the distribution of vegetation types over the earth is correlated with climate has long been documented through extensive surveys and maps. "Vegetation type" is here taken to mean morphological and behavioral attributes of a plant that clearly distinguish it from others, such as woody versus herbaceous, needle-leaved versus broad-leaved, deciduous versus evergreen, etc. By "climate" is meant a long-term statistical characterization of the temperature, precipitation, and general weather patterns of a region. Given the undeniability of the correlation between vegetation types and climate, scientists have naturally wanted to ask: what climate attributes are sufficient to summarize the climate regime and to predict corresponding vegetation forms? And if such prediction is possible, why do those particular vegetation forms arise within those climate regimes? Delving even deeper,

since the real-time interaction between vegetation and climate is through, on the one hand, weather impacts on vegetation processes, and, on the other hand, vegetation exchange of gases and energy with the atmosphere, is it possible to predict not only vegetation form but also function, that is, real-time activity, given the vegetation and climate or only one of the two? We wonder: can vegetation be predicted not only through correlational relations, but through physically, climatically determined constraints on plant processes that drive their evolution?

The guiding framework of these questions is that somehow the plants found in a particular climate regime are best evolved for that climate, whether that means they have a competitive advantage for survival compared to other plant types, or that they can best maximize productivity in that climate, or both; or perhaps there is some other criterion that determines the domination of particular vegetation types in a particular climate type. Ultimately, the goal here is to answer the question about real-time activity, and in trying to do so, it is found consultation must be done of a variety of disciplines that have approached the question from different angles. Below, in reviewing these developments it is found that the critical link among disciplines and spatial and temporal scales is forced when plants experience soil moisture deficits.

4.1.1 Correlational schemes

Simple climate indicators that summarize the availability of water and energy have yielded emphatic mapped patterns that closely approximate observed distributions of vegetation types, providing a convincing argument that plant form ultimately must be adapted to climate. Examples of these climate indicators are mean annual temperature

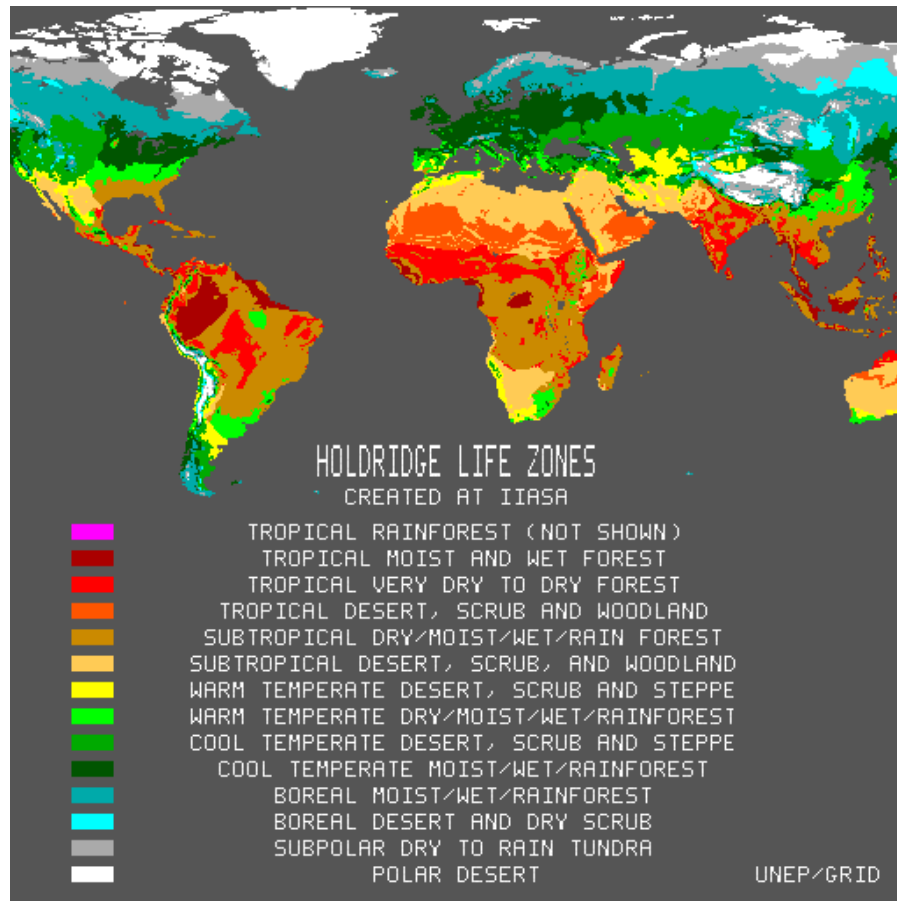


Figure 4.1: Holdridge Life Zones, United Nations Environment Program

and precipitation, growing season length, ratio of potential evapotranspiration to water availability, and similar others. Such correlations schemes have shown good predictive power of the occurrence of vegetation type at the biome scale (Holdridge, 1967; Whittaker, 1975; Woodward, 1987) and to the scale of finer topographic variations within a region (Stephenson, 1998). Holdridge's life zones (1967) continue to be popular for generating global maps of vegetation types, as in Figure 4.1.

Not only plant form but also function has been observed to be adapted to climate,

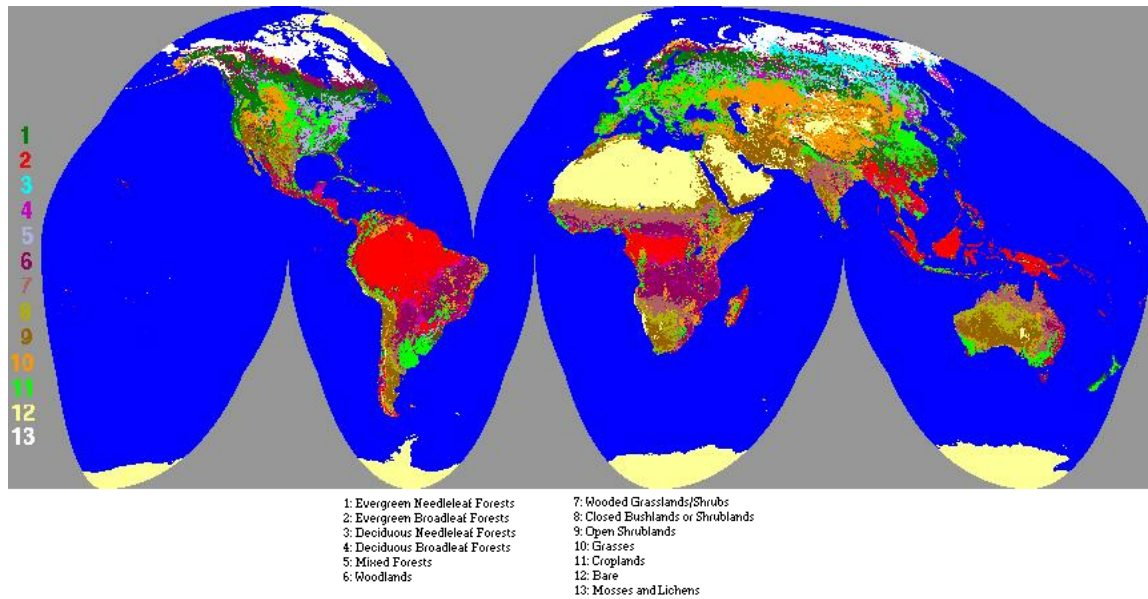


Figure 4.2: NDVI-based vegetation classification (Defries & Townshend, 1994).

in terms of the intensity with which plant processes like transpiration and photosynthesis occur. In Figure 4.2, a map of the Normalized Difference Vegetation Index (NDVI), a satellite data indicator of photosynthetic activity, yields vegetation patterns very like that of the Holdridge diagram. Churkina and Running (1998) have perhaps produced the ultimate refinement of these correlational schemes by classifying climate indicators using fuzzy set theory (a means of categorizing with probability distributions rather than with discrete sets) and correlating these with simulated potential vegetation net primary productivity.

4.1.2 Climatological simulation models

Thus, the correlation between climatic regime, plant form, and plant function is undeniable. Climatologists have taken the issue of plant function further by relating these

correlation schemes to the theory that water-limited vegetation will tend to support the maximum leaf area as allowed by the water and energy supply. This theory derives from the Principle of Limiting Factors or Liebig's Law of the Minimum, a simple paradigm in plant ecophysiology (Jones, 1992) and ecosystem ecology (Aber and Melillo, 1991). It is usually used to refer to resource limitations on growth, and may be refined (or criticized) to account for changes in efficiency of use due to plant acclimation (Sinclair, et.al., 1993) , or to describe interaction among resources or driving controls (Antonius Van Den Burg, 1998). For example, the rate of carbon assimilation is limited by the slower among the biochemical reactions involved in carboxylation, as well as by stomatal control over diffusion of carbon dioxide into the leaf; transpiration is limited by evaporative demand by the environment or by the availability of soil moisture; at the landscape scale, the gross levels of transpiration are limited by both the leaf-level limitations as well as the extensiveness of plant cover. Meanwhile, interactions among factors can result in simultaneous limitation, rather than limitation by only a single driver at a time. Climate (water, irradiance, temperature), of course, is not the only limiting factor in vegetation distribution and composition, as nutrient availability and processes such as herbivory and fire also are controllers; however, climate still places the upper and lower bounds on the plant physiological processes and hence productivity and overall leaf area.

Based on the idea of environmental constraints (resources, climate), geographic simulation models at coarse spatial and temporal scales have succeeded in predicting the leaf area index (LAI) over the globe for most terrestrial ecosystems with a homogeneous leaf area distribution (Nemani and Running, FOREST-BGC, 1989; Woodward, 1987; Neilson's

MAPSS model, 1995; Foley's IBIS model, 1996; Prentice, et. al.'s BIOME1 model, 1992). These biophysical-biogeographic models simulate the water balance with varying degrees of detail in the hydrology, physiology, and carbon dynamics, and update the leaf area and/or vegetation cover type to achieve an equilibrium level. For those models that are applied at the continental and global scale, accuracy tends to be poorest in arid and semi-arid regions that are subject to shifts due to disturbance or interannual climate variation and drought. These models take the vegetation-climate link the next step up from mere classification by simulating productivity and the location of vegetation types, but they must still rely on knowledge beforehand of the functional characteristics (e.g. temperature tolerances, maximum photosynthetic capacity) of each vegetation type. Could those functional characteristics be further predicted purely from climate?

4.1.3 Ecohydrologic optimality: soil moisture, vegetation, and climate

The scientists of the previous two sections have approached the vegetation-climate questions from the angle of plant ecophysiologicals, stressing the details of the plants, particularly the leaf form. By contrast, hydrologists have sought to detail the dynamics of soil moisture with respect to climate, with generally coarse bulk parameterizations of vegetation activity with little regard for plant form; their models are often used by climatologists to do simulations that include a water balance. Hydrologists who have sought to delve deeper into the interaction between vegetation and soil moisture are few, but their work is worth understanding, because of their analytical approaches and the insights these yield.

In 1978, Peter S. Eagleson, a hydrologist at MIT, took an entire issue of the journal *Water Resources Research* to publish in seven sections a treatise on the relationship between

climate, soil, and vegetation (Eagleson, 1978abcdefg). He laid out fully the dynamics of precipitation and soil moisture processes as represented by hydrologists (stochastically and physically), and discussed in detail the importance of plant rooting depth in affecting the water balance. He developed analytical solutions for predicting the annual water yield of a region. This work eventually lead him to examine the role of vegetation in water-limited systems, hypothesizing that in the very long-term scale of climatic equilibrium, both soil and plant parameters coevolve to achieve simultaneous soil moisture holding capacity and plant cover to correspond to the climate regime (Eagleson, 1982ab). The climate regime is characterized in terms of mean annual precipitation and potential evaporation. His long-term, analytical equilibrium solutions yielded non-dimensional relations (a common practice in fluid dynamics) for predicting vegetation cover and function ("transpiritivity") and soil porosity from climate. This work even allowed him to predict vegetation functionality, such as deciduousness versus evergreen. Since the amount of vegetation cover is limited by the amount of available soil moisture, Eagleson developed this work further finally for savanna ecosystems in particular (Eagleson, 1985), as these ecosystems are defined by seasonal water limitation and scattered trees that do not close over the landscape. Eagleson took cues from Walter (1971), a plant ecologist who laid down the classic theory about savannas: that the two distinct plant forms, tree and grass, coexist in savannas due to niche partitioning of soil moisture by shallow rooting depth for grasses, and deep roots for trees. Eagleson worked his theory to accommodate the two plant forms in order to predict their relative cover over the landscape, yielding again non-dimensional relationships for such prediction from climate.

A few tests of the vegetation cover predictions against real data (Nylsvley, South Africa and the Jonglei Canal in the Sudan) fall astonishingly on Eagleson's curves. In short, he seems to have achieved analytically what climatologists have done through massive simulations to predict LAI, and he solved simultaneously for soil parameters, rather than having them be exogenous. However, because of the massiveness of Eagleson's work, the unconcern of most hydrologists for vegetation details, and the publication in *Water Resources Research*, which few ecologists read, his work has few successors. Nemani and Running (1989) coming from the plant ecophysiology/climatology community took inspiration from Eagleson's work to do more detailed ecosystem simulation to predict soil-leaf area equilibrium for forests. There has been no follow-up work. More recently, Hatton (1997) was moved to write an essay lamenting the neglect of Eagleson's theories. The pitfall for Eagleson is probably that he was delving into the realm of climate and evolution, such that his theories have little direct use for the hydrological community. Meanwhile, his parameterization of the plants relies on a crude bulk quantity, their "transpiritivity," the relation of which to actual plant controls (hydraulic and stomatal conductances) is unclear, and his quantification of plant cover has no clear relation to plant leaf area, such that his theory is difficult for the plant ecophysiological community to relate to plant form and functioning. Finally, as a long-term, equilibrium end-point solution with only mean annual indicators for climate, Eagleson's theory is not useful for those scientists trying to investigate mechanistic processes. The predictions that Eagleson made for Nylsvley and the Jonglei Canal still are valid, but how his simple parameterizations relate to real processes to justify their predictive power must be better understood.

Rodriguez-Iturbe

Ignacio Rodriguez-Iturbe and co-workers moved the research from simple theoretical modeling to address vegetation-soil moisture equilibrium by incorporating more process-based modeling of the water balance and vegetation response to water stress (Rodriguez-Iturbe, et.al., 1999; Laio, et.al., 2001a; Laio, et.al., 2001b). They combined hydrologists' stochastic modeling of climate (rainfall regime) and soil moisture balance with a simple linear model of evapotranspiration as a function of soil moisture in order to arrive at an analytical solution for the probability density function (pdf) of soil moisture (relative to saturated moisture content). The predicted pdf's are not merely for the mean annual climate but can be solved for a particular season of the year when the rainfall statistics follow a marked-Poisson distribution during the period. The model of evapotranspiration incorporates a linear decline in evapotranspiration between soil moisture points where plants experience the onset of stress, s_* , and wilting, s_w , following the evidence observed in leaf gas exchange by Gollan, et.al. (1985) and subsequently in other studies (Gollan, et.al., 1992; Schulze, et.al., 1994). Plant access to soil moisture is determined by a bulk rooting depth, and plants are further characterized as having a maximum evapotranspiration rate, $E_{\max}$, under unstressed conditions. The soil moisture pdf's then allow the researchers to make predictions about the time courses of soil moisture dry-down (or wet-up), and to formulate various indicators of vegetation water stress (how frequently the soil moisture is below the stress point) for different soils, vegetation characteristics, and rainfall regimes (Porporato, et.al., 2001). With these tools, they could then ask questions about plant adaptations to climate: given a certain probabilistic behavior of soil moisture and plant characteristics at

a particular site, can the soil moisture pdf's and water stress measures explain the functionality, rooting depth, and competitive advantage of different species? Where different functional types of plants coexist, how may one expect their relative dominance to shift with interannual climate variation?

Rodriguez-Iturbe and co-workers (Laio, et.al., 2001b) applied their probabilistic soil moisture equilibrium model to data from two savannas and a grassland: a tropical warm savanna in Nylsvley, South Africa (Scholes and Walker, 1993), a brushland savanna in La Copita, Texas, and a short-grass steppe in Colorado. They calculated the soil moisture pdf's for these sites with different rainfall regimes and soil textures, and for species with different rooting depths and water use strategies, and compared stress levels for the different species. These characterizations yielded interesting insights into the tree-grass coexistence in savannas and the grass distribution in the short-grass steppe. In Nylsvley, similar rooting depths of two woody and two herbaceous species but different water use strategies (maximum transpiration rate, stress and wilting points) yield the same water stress levels for each species, thus affording their coexistence in a savanna. At La Copita, interannual variation in climate leads to fluctuation in the competitive advantage (trade-off in stress levels) between trees and grasses, leading to unstable coexistence. In Colorado, the short-grass species *Bouteloua gracilis* was shown to prefer different soil textures for different rainfall regimes. The researchers conclude with avenues for future research to account for the roles of productivity, interannual climate variation, and the evolutionary dynamics of vegetation.

There are some points to note before trying to apply or critique this model. The

model is valid for application to a season that can be considered homogeneous with respect to rainfall dynamics and vegetation behavior (precipitation obeys a marked-Poisson distribution). If one desires to treat seasonal variation, then the model should treat each season separately. A pitfall of doing this is that the model does not take into account some prior initial condition set by the previous season, and some seasons may be too short to come to equilibrium with the climate regime that characterizes that season.

In formulating the equations for evapotranspiration, for analytical tractability, Rodriguez-Iturbe and co-workers lump soil evaporation and plant transpiration together. Also, the plant parameters, rooting depth and critical transition points for plant response to soil moisture – the “onset of stress” and the “wilting point” – must be determined ahead of time – they are not solutions of the model with respect to the climate regime and soil physical characteristics, unlike with Eagleson, in which the plant parameters are part of the solution.

Finally, the model is not driven by energy. This is not a liability of the model if the season being treated is homogeneous with respect to available energy and plant behavior. However, this is an important point to distinguish if energy availability strongly defines each season.

This elegant work by hydrologists is a significant step in describing vegetation adaptation to climate, and in particular the matching of vegetation function to rainfall regime in water-limited systems. Note that this probabilistic equilibrium model was used to provide characterizing indicators through their soil moisture pdf’s and water stress points, to provide a means of interpreting vegetation strategies and composition in ecosystems with

respect to soil moisture. The model is not meant for predicting instantaneous fluxes. It is fundamental in the description of basic soil moisture processes but is not process-based with respect to vegetation (though it vastly adds to the minimal parameterizations that have been done by hydrologists to date). The next step completely to link vegetation and climate must include the role of available energy and the basic processes of vegetation gas exchange: photosynthesis and transpiration. These processes occur not at the landscape but at the leaf level.

4.2 Leaf scale: ecophysiologicals and stomatal conductance

Plants exchange carbon dioxide and water vapor with the atmosphere via gas exchange through pores in the leaves, called stomates or stomata. Gas exchange through an individual stomate occurs through the process of diffusion, i.e. is a function of the physical dimensions of the stomatal aperture, the concentrations of the gases within and outside the leaf, and the relative diffusivities of those gases. The stomatal aperture is subject to opening and closing, which is partially explained by electron transfer interactions, which the reader can find described in detail in textbooks by Jones (1992) and Nobel (1991); note, however, what motivates stomatal opening and closing is not well-known (more detail below). The gas concentrations are in turn subject to ideal gas law relations to temperature and pressure, biochemical processes within the leaf acting as sources or sinks, and micrometeorological processes affecting the boundary layer outside the leaf. Gas exchange at the leaf level is not simply the cumulative parallel conductances of the individual stomata, because conductance through the leaf boundary layer is not in fact uniform across the pores, but the lines of flux

converge on the pore due to three-dimensional diffusion, such that there is an extra “end-effect” resistance around each pore. Furthermore, stomata do not all act in unison across the leaf surface (Mott and Buckley, 2000). In general, however, the conductance or resistance of gas flux is measured and modeled on a per leaf area basis, not by individual stomate. In the plant physiological literature, “stomatal conductance” is generally used to mean leaf stomatal conductance of water vapor, the common symbol and units being molar flux, g_s [mol-H₂O m⁻² s⁻¹]; atmospheric scientists report this conductance in length per time [e.g. m s⁻¹].

While the simple process of diffusion can be described through straightforward physics, the controls on the stomatal aperture are not completely understood. The issues surrounding the difficulties of modeling leaf water potential and the hormone abscisic acid were reviewed in Chapter 1. Hypotheses about the behavior of the stomata range from teleological strategies, to passive cellular physical reactions, to active biochemical responses. Teleological strategies include “goals” of the plant (not mechanistically defined), such as protection against catastrophic cavitation, (Sperry, 2000; Nardini and Salleo, 2000), or maintenance of level of transpiration (Monteith, 1995; Mott and Parkhurst, 1991). Environmental responses through cell membranes could be simply passively physically driven (see Nobel, 1991). Biochemical responses could include active hormonal signals related to root sensing of soil moisture deficits (Tardieu, 1993; excellent review by Sauter, et.al., 2001). Because the stomata are coordinating the loss of water vapor on the one hand and the acquisition of carbon dioxide on the other, the processes of both transpiration and photosynthesis must be included in any modeling of stomatal conductance. It is clear that the

flux of gases through a stomate or whole leaf is a function of internal physiology, ambient environmental conditions, and the energy balance of the leaf as affected by all these. Below a review is provided of the history of the models that have attempted to capture these influences. There are several classes of models of stomatal conductance, ranging from simple phenomenological (Jarvis-type), to empirical (Ball-Berry, 1987; Leuning, et.al., 1998; Collatz, et.al., 1991), to semi-mechanistic simulation (Baldocchi, 1994; Nikolov, et.al., 1995; Su, et.al., 1995), to optimality models (Cowan, 1977; Cowan and Farquhar, 1977; Mäkelä, et.al., 1996; Givnish, 1986; Friend, 1995).

4.2.1 Empirical models

Jarvis model

The early model of Jarvis (1976) is a simple, empirical model that has been used extensively in climate and weather models to calculate stomatal conductance. The simple multiplicative form of this model now is often referred to as a “Jarvis-type model.” A maximum conductance value, g_0 , is modified by fractional scaling factors, or “stress factors,” that are independent functions (response curves) of photosynthetically active radiation, PAR, air temperature, T_a , vapor pressure deficit, VPD, soil water potential, Ψ , and molecular diffusivity and carbon dioxide concentration, C (Equation 4.1):

$$g_s = g_0 \cdot f(PAR) \cdot f(T_a) \cdot f(VPD) \cdot f(\Psi) \cdot f(C) \quad (4.1)$$

These response curves must be empirically tuned, and any variety of equations for curve-fitting that describes these behaviors is possible. The curves shown in Figure 4.3 are illustrative, giving typical ranges for the driving environmental variables and the type of response

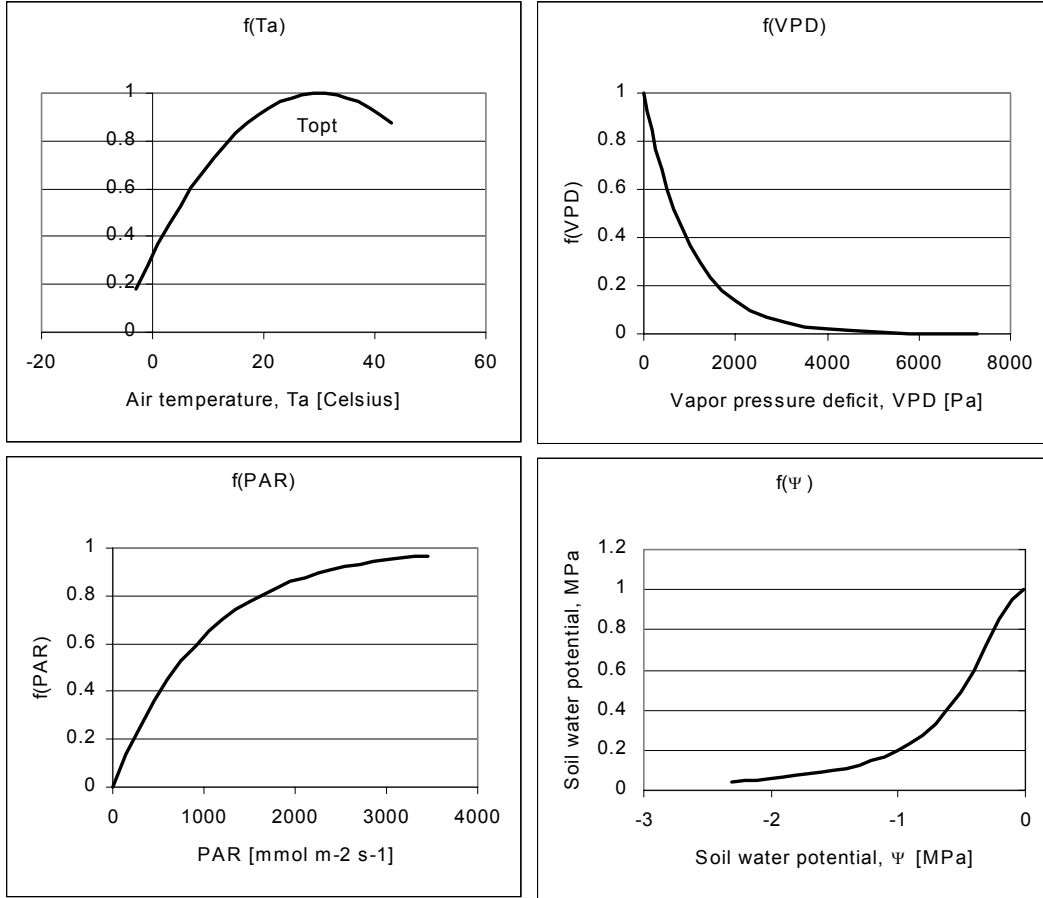


Figure 4.3: Empirical responses of stomatal conductance to individual meteorological drivers (air temperature, T_a ; vapor pressure deficit, VPD; photosynthetically active radiation, PAR; soil water potential, Ψ) in a Jarvis-type model.

behavior that should be captured. For example, the light response should have approximately a linear response to PAR or PPFD and then saturate. The temperature response should have some optimum, possibly some plateau. The vapor pressure deficit response should decrease with increasing deficit, possibly asymptotically. And the soil moisture response should be highest under saturated soil moisture conditions and flatten out beyond the wilting point. There is no explicit treatment of the biochemistry of photosynthesis or the processes of diffusion. Such simple factorization works well enough operationally due to its empirical nature but does not describe the mechanisms involved, particularly the interactions that occur among factors, such as feedbacks of transpiration to vapor pressure deficit or the interaction between stomatal conductance and assimilation.

Semi-mechanistic models

The next class of models attempts to describe the interactions among driving variables and processes by direct incorporation of their relations in a physical-statistical equation (physical in the sense that units have meaning), not by treating them as merely embedded within independent scaling functions. These may be viewed as multivariate statistical models. The Farquhar-von Caemmerer/Ball-Berry combination as mentioned earlier is one such model, which is reviewed here, with some variants.

In the model of Ball and Berry (1987), stomatal conductance is recognized as directly correlated with assimilation and relative humidity and inversely correlated with CO₂ mole fraction at the leaf surface:

$$g_s = m \cdot \frac{A \cdot RH}{c_s} k_g (S) + g_0 \quad (4.2a)$$

where:

g_s = stomatal conductance of water vapor [$\text{mol m}^{-2} \text{s}^{-1}$]
 A = CO_2 assimilation rate [$\text{umol m}^{-2} \text{s}^{-1}$]
 RH = relative humidity [fraction]
 c_s = mole fraction of CO_2 at the leaf surface [umol/mol]
 m = empirical coefficient
 k_g [dimensionless] = sensitivity of stomatal conductance to soil water content, w_s
 S [any units] = soil water content

The response to soil water content, k_g , is generally neglected for well-watered situations and must be empirically determined.

Ball and Berry found through experiments over a range of conditions in each variable that the slope, m , and intercept, g_0 , remain fairly constant for a given plant species. They found for *Glycine max*, $m = 9.31$, $g_0 = 0$. However, a survey of the literature by Xu and Baldocchi (2002, in preparation) reveals a wide range in the Ball-Berry slope across more than 20 species, from as low as 3 for corn (Collatz, et.al., 1992) to as high as 18 for sugar maple (Ellsworth and Reich, 1993) and a montane herbaceous species (Wohlfahrt, et.al., 1999). The overall mean, unstratified, is 9.8 with a standard deviation of 3.8, and the variation does not show particular trends among functional types. Within species, m can vary considerably (Leuning, et.al., 1995), not always for clear reasons. Some investigators looked at the role of stand age (Falge, et.al., 1996, old stand m is about half that of a young stand of *Picea abies*), seasonal variation (Xu and Baldocchi, 2002, submitted, constant m across seasons including drought for *Quercus douglasii*), and environmental conditions (Medlyn, et.al., 2001, elevated CO_2 only has an effect on m under water-stressed conditions). Experimental error with the leaf gas exchange technique may also be responsible for the observed variation, since some researchers overlook the phenomenon that the

leaf stomatal conductance lags assimilation rate in coming to equilibrium with new environmental conditions (Xu, personal communication). In general, given this variation in the Ball-Berry slope, it is clear that this empirical model offers the benefit of simplicity but that the fitted values, although constrained within an order of magnitude, cannot be extrapolated without some caveats.

The simplicity of the Ball-Berry model is worth comment, given that it is able to describe stomatal conductance fairly well, despite variations in m , even while the equation is not mechanistic. The use of relative humidity rather than vapor pressure deficit (VPD) has been subject to some scrutiny, since the process of diffusion is a function of a driving potential through the stomates; it seems that VPD should be the preferred, more mechanistic explanatory variable. Ball and Berry address this issue, noting that their measurements of g_s vs. VPD at different temperatures showed that g_s decreased in sensitivity to VPD at higher temperatures, and this may be due to the changing mole fraction of water vapor at higher temperatures. Since relative humidity scales vapor pressure, P_v , for changes in the saturation vapor pressure, $P_{v,sat}$ (since RH is a ratio of the two), it incorporates this changing sensitivity.

$$VPD = P_{v,sat}(T) - P_{v,a} \quad (4.3)$$

$$RH = \left(\frac{P_{v,a}}{P_{v,sat}(T)} \right) \quad (4.4)$$

$$\frac{VPD}{P_{v,sat}(T)} = \left(1 - \frac{P_{v,a}}{P_{v,sat}(T)} \right) = 1 - RH \quad (4.5)$$

From Equations 4.5, one can see as $VPD \rightarrow 0$, then $RH \rightarrow 1$ (max RH), and as $VPD \rightarrow P_{v,sat}$ (i.e. $P_{v,a} \rightarrow 0$), then $RH \rightarrow 0$ (min RH). So VPD and RH are inversely related. From their data, therefore, Ball and Berry can conclude that stomata respond to relative

humidity. I also remark that it is clear that stomata close to counteract the greater driving potential under higher VPD , in which case VPD would have to be in the denominator of the equation; then when VPD goes to zero, the value of g_s would blow up. Having relative humidity in the numerator makes for a stable equation, while incorporating the multiplicity of effects that accompany changes in VPD (temperature sensitivity, stomatal closure in dry air). Since this is a simple empirical equation, using relative humidity as just the converse of VPD is conceptually acceptable within this framework. Why it should work so well must be the subject of further research on detailed mechanisms.

Some researchers have posed variations on the Ball-Berry model but do not depart fundamentally from its form. Leuning (1995) substituted VPD into the denominator of a version of the Ball-Berry equation:

$$g_s = \frac{\alpha_L A}{(c_s - \Gamma_*) \left(1 + \frac{VPD}{VPD_0}\right)} + g_0 \quad (4.6)$$

where:

α_L = slope for the Leuning model
 Γ_* = CO₂ compensation point [$\mu\text{mol/mol}$]
 VPD = vapor pressure deficit [Pa]
 VPD_0 = some threshold value of VPD

Again, as mentioned above, since VPD declines as relative humidity increases, obviously putting VPD in the denominator performs the same descriptive function as putting RH in the numerator. The Leuning model is awkward, though, in that it requires adding 1 to VPD (scaled by some unknown threshold value) in order to avoid the possibility of zero in the denominator, and this makes fitting the model more difficult. Mathematically, as an empirical model, there is no advantage over the Ball-Berry model, since VPD and RH are inversely related. Consequently, this model adds complications without improving results

of the Ball-Berry model.

Aphalo and Jarvis (1993) pose a variation on the Ball-Berry model, using fractional response functions to VPD and leaf temperature in additive form to replace RH in the Ball-Berry model. This added empiricism is subject to the same data difficulties of Jarvis-type models, and though it may improve on statistical fits due to having more terms, like the Leuning (1995) model, it is only a variation that does not depart conceptually from the Ball-Berry model.

In general, the Ball-Berry model is not only simple and largely consistent, but it is practically useful, since measures like relative humidity and c_s are measures external to the leaf that are relatively easily obtained from meteorological data. However, the assimilation rate, A , must be obtained from other models of photosynthesis, and other interactive effects are hidden here.

Interaction between stomatal conductance, g_s , and assimilation, A

Stomatal conductance, g_s , and assimilation rate, A , feedback to each other, as stomatal conductance has been shown to be positively correlated with assimilation while being influenced by other environmental factors as well, and assimilation is necessarily limited by diffusion as controlled by the stomates. Numerical models have been used to capture these feedbacks between biochemical processes on the one hand and physical (diffusion, micrometeorological) processes on the other. Given the instability of numerical models, several researchers coupled the Farquhar and von Caemmerer (1982) model of photosynthesis in steady-state with a diffusion equation for CO_2 , and the Ball-Berry (1987) model of stomatal conductance to derive an analytical solution for assimilation, A , (and therefore also c_i and

g_s) (Collatz, et.al., 1992; Baldocchi, 1994; Nikolov, et.al., 1995; Su, et.al., 1996). The resulting expression requires as its environmental drivers ambient CO₂ mole fraction, c_a , relative humidity, RH, irradiance, I, and the leaf boundary layer conductance of CO₂, g_b . This solution is useful for biophysical models to predict fluxes from readily available meteorological drivers. This coupling of the Farquhar-von Caemmerer (1982) model of assimilation and the Ball-Berry (1987) model of stomatal conductance has yielded close imitation of gas exchange measurements under non-water stressed conditions (Baldocchi and Meyers, 1998; Nikolov, et.al., 1995; Su, et.al., 1996).

Modifying models for drought stress

Because the mechanisms that induce stomatal closure under drought stress are not clearly known (as reviewed in Chapter 1) researchers have experimented with modifying their empirical equations with scaling factors relative to soil moisture or leaf water potentials. This is generally done by mapping some range of water potentials (from a critical stress point to an unstressed point) to 0-1, and then multiplying this fractional factor by the conductance equation or by an assimilation equation. This is justified, partly, because observations have shown a fairly linear response of maximum stomatal conductance between these water potential points, with an upper threshold reached when there is no soil moisture deficit (Figure 4.4). This approach has been applied to the Jarvis model (Jarvis, 1976), and is even embedded in an optimality model (modifying assimilation) (Friend, 1995). It is also used to formulate an indicator of water stress in the hydrological model of Rodriguez-Iturbe, et.al. (2001) and the savanna model of Siomoni, et.al. (2001). In the model SiB2, Sellers, et.al. (1996a, 1996b) use an exponential function of soil moisture to reduce the slope and

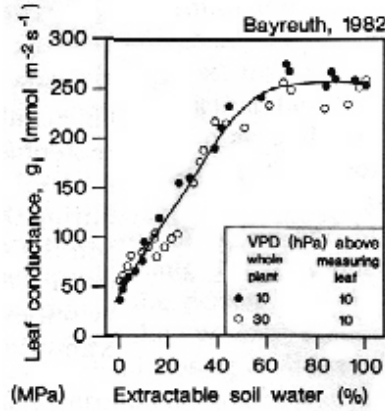


Figure 4.4: Leaf conductance vs. soil moisture in dry and moist air for *Nerium oleander* (Schulze, 1994a).

intercept of the Ball-Berry stomatal conductance equation, and to reduce photosynthetic capacity in the Farquhar-von Caemmerer model of assimilation. The curves used have not actually been explained in publication, but are tuned operational fixes that seem to achieve desired results (Joseph Berry, personal communication).

These fixes to stomatal conductance models are simple but highly empirical, especially since few species have well-defined water stress points. The fact that the slope and the intercept of the Ball-Berry equation are not constant leads us to ask why they vary and how much error can result from slight inaccuracies in these parameters. Rather than merely posing adjustments to the Ball-Berry model, can one do better?

4.2.2 Optimality models

A completely different class of theories of stomatal control are optimality theories, based on adjustment of resource budgets to achieve some objective function, such as maximizing carbon gain or minimizing water loss, or some combination of the two, e.g.

maximizing some measure of water use efficiency (WUE). These are top-down, economic theories that view a plant's strategy for fitness as a whole, subsuming individual mechanisms as a suite of behaviors that serve optimization. Cowan and Farquhar (1977) and Cowan (1982) performed the early theoretical investigations, subsequently motivating further work by the Finnish team of Hari, Mäkelä, Berninger and others (various papers, 1986, 1993, 1996, 1999, 2000); Lloyd (1991); and Givnish (1986) and Friend (1995). The models developed by these workers all treat diffusion of CO₂ and H₂O vapor, and vary in sophistication in their modeling of carbon assimilation or leaf boundary layers. Where they differ most critically is in their definition of optimality. To understand these differences and why they cause difficulty, the general framework for an optimality model of stomatal conductance is laid out below, and then the variants by the above researchers are pointed out.

Budget equations of leaf gas exchange

Optimality modeling is based on formulating budget equations, with constraints, and an objective function. Below are the basic budget equations for leaf gas exchange and common constraining assumptions about them. (The reader is advised to read Appendix D on Units and Dimensions in Leaf Gas Exchange for a solid framework of the nomenclature here).

Leaf water vapor budget: transpiration by diffusion Leaf transpiration may be expressed as a conservation equation, in which the leaf water content is subject to inputs from the stem source and outputs through diffusion through the stomates and

through the leaf cuticular layer:

$$l_i \frac{dW_i}{dt} = E_{mesophyll} - E_{leaf} \quad (4.7a)$$

$$l_i \frac{P}{RT_{leaf}} \frac{dw_i}{dt} = E_{mesophyll} - E_{leaf} \quad (4.7b)$$

where:

l_i = leaf internal space thickness [m]

W_i = leaf interstitial space water content (density) [mol m⁻³]

w_i = leaf interstitial space partial pressure [mol mol⁻¹]

$E_{mesophyll}$ = flux of water vapor into the leaf internal space from the mesophyll [mol m⁻² s⁻¹]

E_{leaf} = flux of water vapor out through stomates and the leaf cuticle [mol m⁻² s⁻¹]

(Positive is flux out of the *leaf*).

The leaf water content, W_{leaf} , is the water vapor in the leaf interstitial spaces.

Conventionally, it has been assumed that the leaf internal water vapor pressure, $w_i = W_{leaf} \frac{RT_{leaf}}{P}$, is always saturated with respect to the leaf temperature, such that w_i varies with the diurnal leaf temperature.

More importantly, the mesophyll water content, W_{meso} , is subject to clear diurnal variation, as has been observed from numerous pre-dawn and mid-day twig xylem water potential measurements, as the mesophyll serves as a form of water storage for the leaves through equilibration with soil water potential at night. Therefore, $E_{mesophyll}$ restricts the supply of water vapor, with both diurnal and long-term trends that track soil moisture. To model $E_{mesophyll}$ requires a model of the hydraulic resistances of the plant to describe the supply of water along the pathway from the soil to the roots and through the stem. The empiricism required in modeling these resistances was discussed in the previous chapter, but it is reiterated here that it has usually been expediently represented as a series of bulk resistances (or even one, whole-plant bulk resistance). The driving forces are the

water potentials from the soil to the leaves to the air. As the plant changes in its level of hydration, those water potentials and resistances are subject to change, making them very difficult to quantify or predict. As it is the purpose here to circumvent the problem of defining $E_{mesophyll}$, no equation is offered here, but the reader is alerted to pay attention to how the problem will be replaced by an optimality approach with respect to stomatal control in later sections.

The flux of water vapor through the leaf cuticle and the stomates, E_{leaf} , comprises the plant's transpiration or overall water use (neglecting loss of water through the stems). The leaf cuticle is an extracellular, continuous polymer membrane, ranging in thickness on the order of magnitude of 0.1-10 μm (Lendzian and Kerstiens, 1991). This layer serves as a barrier to the movement of water, solutes, and gases, allowing the plant to establish stomatal control over these fluxes, but it is not impermeable, such that the losses of water vapor through the cuticle are significant enough to be accounted for. Cuticular loss can be 10-50% of the diffusion of a leaf with fully open stomata in mesophytes (Larcher, 1980). Lendzian and Kerstiens (1991) provide an extensive review of permeability of the cuticle to various gases in many plant species, finding the cuticular conductance (or "permeance") to range from $8.2 \times 10^{-7} \text{ m s}^{-1}$ in *Schefflera actinophylla* to a maximum of $8 \times 10^{-5} \text{ m s}^{-1}$ for angiosperms (at 25 °C and standard atmospheric pressure, 101.33 kPa, these values translate to 0.03-3.3 $\text{mmol m}^{-2} \text{ s}^{-1}$). Pine trees range $0.25 - 3 \times 10^{-5} \text{ m s}^{-1}$ (0.1-1.2 $\text{mmol m}^{-2} \text{ s}^{-1}$). The coefficient of variation of a species can vary as much 20% to 50%, due to the inhomogeneity of the cuticle and also due to dependence of the permeance on the moisture content of the cuticle (directly correlated with relative humidity).

Flux through the stomates and cuticle occurs via diffusion, with the resistances through the stomates and cuticle in parallel, with these then in series with the leaf boundary layer resistance. Therefore, E_{leaf} including all resistances is:

$$E_{leaf} = \frac{1}{\left(\frac{1}{r_s} + \frac{1}{r_{cuticle}}\right)^{-1} + r_b} (w_i(T_{leaf}) - w_a) \quad (4.8)$$

where w_a [ppm] is the mole fraction of water vapor in the ambient air, $r_{cuticle}$ [$\text{mol}^{-1} \text{ m}^2 \text{ s}^{-1}$] is the leaf cuticular resistance to water vapor, r_s [$\text{mol}^{-1} \text{ m}^2 \text{ s}^{-1}$] is stomatal resistance to water vapor, and r_b [$\text{mol}^{-1} \text{ m}^2 \text{ s}^{-1}$] is the leaf boundary layer resistance to water vapor, a function of wind speed. The cuticular resistance could possibly be changing as a function of time and ambient humidity. In general, the cuticular resistance of a plant species does not vary phenologically and may be considered constant with respect to time. The stomatal resistance, r_s , has already been discussed extensively in Section 4.2, in terms of its inverse, conductance. It is the response of r_s to soil moisture deficits that scientists do not know how to model mechanistically. The above equation for leaf transpiration, Equation 4.8, is an evolution equation (rather than a budget equation).

The boundary layer resistance is a function of the leaf size, l_{leaf} , wind speed, u_t , the diffusivity of the gas in air, D_{gas} , the kinematic viscosity of air, $\nu_{k,a}$, and the temperatures of the leaf surface and the air, $T_{l,surf}$ and T_a , as related by the Sherwood number, Sh :

$$r_b = \frac{D_{H_2O}(T_a) \cdot Sh(u, l_{leaf}, \nu_{k,a}, D_{H_2O}, T_{l,surf}, T_a)}{l_{leaf}} \quad (4.9)$$

For details about calculating the Sherwood number and boundary layer resistances in general, please see Appendix D. Leaf boundary layer modeling is reviewed by Schuepp (1993) and Grace, et.al. (1981), with textbook overviews by Monteith and Unsworth (1990), Camp-

bell (1998), and Jones (1992). Definitions of non-dimensional quantities for heat and mass transfer are summarized in Kreith and Bohn (2001) and Incropera and DeWit (2002).

Plant ecophysologists have traditionally focused more on the evolution equation when considering just well-watered plants. To account for water stress due to soil moisture deficit, it is critical to understand how the source term, $E_{mesophyll}$, limits the supply of water and how the stomatal control by the plant via r_s reflects that limit. Since the desire here is to bypass the messiness of modeling $E_{mesophyll}$, the following important assumption will be made: that the limits on $E_{mesophyll}$ are a reflection of optimal behavior of the plant with respect to utilization of soil moisture, which is in turn reflected by the constraint by r_s on E_{leaf} . It is assumed that r_s adjusts quickly to account for limits to soil moisture supply, such that, at the measurable time scales for stomatal control, the leaf interstitial space soil moisture content reaches steady-state between supply and loss.

If steady-state is assumed to be quickly reached at the time scales of interest (measurement rate of half-hourly, see Allen and Percy (2000) for study of response times under fluctuating light environments; review in Percy, 1996), then $dW_{leaf}/dt = 0$ and the leaf water vapor conservation equation 4.7a becomes:

$$E_{leaf} = E_{mesophyll} \tag{4.10}$$

At the subdiurnal time scale, changes in soil moisture due to transpiration lag these fluxes, but at the time scale for optimization against soil moisture use, these fluxes are directly equal to soil moisture losses from transpiration, as will be seen later.

Leaf carbon dioxide budget. The leaf carbon dioxide budget may be expressed as the changing concentration inside the leaf, as driven by diffusion from the at-

mosphere as a source into the leaf (A_d) and the biochemistry of photosynthetic assimilation (including dark respiration) as the sink of CO_2 inside the leaf (A_b):

$$l_i \frac{dC_i}{dt} = l_i \frac{P}{RT_{leaf}} \frac{dc_i}{dt} \quad (4.11)$$

$$= A_d(r_{leaf, \text{CO}_2}, c_i, c_a) - A_b(c_i, PAR, T_{leaf}, V_{c\max}) \quad (4.12)$$

where:

All variables are functions of time.
 l_i = leaf internal space thickness [m]
 C_i, c_i = intercellular CO_2 concentration [mol m^{-3}] and mole fraction [ppm]
 c_a = ambient CO_2 concentration [ppm]
 PAR = photosynthetically active radiation [W m^{-2}]
 $A_d(g_{l, \text{CO}_2}, c_i, c_a)$ = supply rate of CO_2 diffusion into the leaf [$\text{mol m}^{-2} \text{s}^{-1}$]
 $A_b(c_i, PAR, T_{leaf}, V_{c\max})$ = consumption rate of leaf internal CO_2 by biochemistry of photosynthesis [$\text{mol m}^{-2} \text{s}^{-1}$]
 $V_{c\max}$ = leaf photosynthetic capacity [$\text{mol m}^{-2} \text{s}^{-1}$]

Diffusion of CO_2 into the leaf is subject to resistances in series due to the leaf boundary layer, r_b , and the stomates, r_s . Resistance to diffusion into the mesophyll, $r_{c,m}$ may also be included, if it is not somehow accounted for in the sink strength of A_b :

$$A_d(r_{leaf, \text{CO}_2}, c_i, c_a) = \frac{c_a - c_i}{1.6r_b + 1.4r_s + r_{c,m}} \quad (4.13)$$

where:

$r_{c,m}$ = resistance to CO_2 flux from leaf internal surface to mesophyll [$\text{mol}^{-1} \text{H}_2\text{O m}^2 \text{s}^{-1}$]
 1.4 = ratio of diffusivities of CO_2 and water vapor in still air at the leaf surface (Monteith, 1973)
 1.6 = ratio of diffusivities of CO_2 and water vapor in laminar flow in the leaf boundary layer (Monteith, 1973)

Photosynthetic assimilation rate, A_b , is best described by the model of Farquhar and von Caemmerer (1982), as has been mentioned earlier. It is driven by the environmental variables c_i , PAR , and T_{leaf} , and by the plant control $V_{c\max}$, and note that it is only

indirectly influenced by r_s through the internal CO₂ concentration, c_i . The full details of the biochemical equations are given in Section 4.2.2 below and in Appendix C.

The common assumption of plant ecophysiology modelers is that stomata adjust quickly such that, at the time scales of most measurements (minutes to a half hour), the leaf internal CO₂ balance can be considered at steady-state; that is, $dC_i/dt = 0$, and the diffusion of CO₂ into the leaf equals the rate of assimilation inside the leaf. Except for a dynamic model of photosynthesis by Pearcy, et.al. (1997), this immediate steady-state assumption has been glossed over in models, although it implies that the leaf internal CO₂ concentration is incidental to stomatal behavior and assimilation rates, rather than being their driver, which is incorrect according to scientists' understanding of carboxylation's concentration-dependent activity. More importantly, acknowledging the temporal budget of C_i provides an explicit explanation of why stomatal conductance is directly correlated with assimilation rate, due to feedback effects: when photosynthesis, A_b , is fast, the faster sink of leaf internal concentration of CO₂, C_i , requires opening of the stomata for diffusive supply, A_d , into the leaf since C_i cannot drop below zero or some other threshold value; when A_b is slow, stomata can close to reduce A_d to match the rate of uptake of C_i (why they should close, however, is not clear, but may be related in this case to minimizing water loss). Thus, stomatal aperture adjusts due to varying rates of assimilation. This mechanistic representation of the time-varying response of C_i helps explain the evidence of Wong, et.al. (1979) and Norman (1982) that stomata adjust to maintain a near-constant C_i/C_a ratio to maintain a diffusive gradient for CO₂ uptake.

Photosynthesis The biochemistry of photosynthesis is now well-known; that is, the Farquhar and von Caemmerer (1982) model of photosynthesis is well-accepted, as was mentioned earlier. Therefore, equations for carbon assimilation, A_b , can be specified without resorting to simplistic Jarvis-type response functions. The Farquhar and von Caemmerer (1982) model is re-stated here, to identify the essential driving variables that will come into play when optimality criteria are later discussed. Full details are provided in Appendix C.

The process of photosynthesis is well-described in textbooks like those by Nobel (1991) and Jones (1992); therefore, the reader should refer to these for more complete definitions of terms. Briefly, the rate of net carbon assimilation by photosynthesis is subject to 5 limiting processes internal to the leaf. These can be viewed as 4 limitations on the rate of carboxylation plus the role of dark respiration in light:

1. Carboxylation when ribulose-bisphosphate (RuBP) is saturated, and O_2 and CO_2 compete for RuBP.
2. Carboxylation when the rate of electron transport/photosynthesis limits re-generation of RuBP.
3. Carboxylation when the rate of triose phosphate transport is limiting.
4. Temperature dependencies of rate constants.
5. The rate of dark respiration in light.

In general:

$$\text{net assimilation} = (\text{carboxylation} - \text{photorespiration}) - \text{dark respiration} \quad (4.14)$$

In photorespiration, for each mole of RuBP oxygenated, 0.5 mol of CO₂ is released, therefore the above relation can be quantified as:

$$A_b = (V_C - 0.5V_O) - R_d \quad (4.15a)$$

$$= V_C (1 - \Gamma_*/c_i) - R_d \quad (4.15b)$$

$$= \min \{W_C, W_j, W_p\} \left(1 - \frac{\Gamma_*}{c_i}\right) - R_d \quad (4.15c)$$

where:

- A_b [$\mu\text{mol m}^{-2} \text{s}^{-1}$] = net assimilation due to biochemistry of photosynthesis
- V_C [$\mu\text{mol m}^{-2} \text{s}^{-1}$] = rate of carboxylation of RuBP
- V_O [$\mu\text{mol m}^{-2} \text{s}^{-1}$] = rate of oxygenation of RuBP
- R_d [$\mu\text{mol m}^{-2} \text{s}^{-1}$] = rate of dark respiration
- Γ_* [ppm] = CO₂ compensation point in the absence of dark respiration
- c_i [ppm] = leaf internal CO₂ concentration
- W_C [$\mu\text{mol m}^{-2} \text{s}^{-1}$] = rate of carboxylation when RuBP is saturated
- W_j [$\mu\text{mol m}^{-2} \text{s}^{-1}$] = rate of carboxylation when electron transport is limiting
- W_p [$\mu\text{mol m}^{-2} \text{s}^{-1}$] = rate of carboxylation when triose phosphate is limiting

For details on the Michaelis-Menten expressions for W_C , W_j , W_p , and ways of expressing R_d , please consult Appendix C. All of the limiting carboxylation rates have the form:

$$W_x = \frac{v_{1,x}c_i}{v_{2,x}c_i + v_{3,x}} \quad (4.16)$$

where $v_{1,x}$, $v_{2,x}$, and $v_{3,x}$ are empirical coefficients that are considered species-specific, and which can vary according to season, temperature, and stresses on the plant. Most critical of these is the coefficient in the numerator, $v_{1,x}$. For W_C , this critical coefficient is the maximum carboxylation rate, V_{max} . For W_j , it is the maximum rate of electron transport, J_{max} . For W_p , it is the rate of triose phosphate utilization, TPU . And among these three, the most widely varying among plant species and by season is V_{max} . In formulating an

optimality model of plant water use, it will be seen that V_{max} is a critical variable in the optimal solution.

Leaf energy budget. Leaf temperature is a critical driver in transpiration and photosynthesis, so estimation of leaf temperature must be done through an energy budget:

$$\frac{dT_{leaf}}{dt} = \frac{\rho_a c_{p,a}}{\rho_l c_{p,l}} (T_e - T_{leaf}) \{g_{HRd} + s_{vap}/\gamma (r_{sd} + r_{bd})\} \quad (4.17)$$

$$T_e = T_e(g_{ld}, l_{leaf}, T_a, P, u, RH) \quad (4.18a)$$

$$= T_a + \frac{\Phi_{iso}(r_{sd} + r_{bd})}{\rho_a c_{p,a}(g_{HR}(r_{sd} + r_{bd}) + s_{vap}/\gamma)} - \frac{VPD/\gamma}{g_{HR}(r_{sd} + r_{bd}) + s_{vap}/\gamma} \quad (4.18b)$$

where:

- l subscript indicates leaf quantity
- T_l = leaf temperature [Kelvin]
- T_e = leaf temperature if it were at equilibrium with the environment [Kelvin]
- T_a = air temperature [Kelvin]
- Φ_{iso} = isothermal radiation [$J m^{-2} s^{-1}$]
- ρ_a = density of air [$kg m^{-3}$]
- $c_{p,a}, c_{p,l}$ = specific heat capacity of air and leaf [$J kg^{-1} K^{-1}$]
- $VPD = P_{v,sat}(T_a) - P_{v,a}$ [Pa]
- γ = psychrometer constant = $P * c_p / (0.622 \lambda_{H_2O})$ [$Pa K^{-1}$] (get values from Jones, 1992, Appendix 3)
- λ_{H_2O} = latent heat of vaporization [$J kg^{-1}$]
- s_{vap} = slope of the saturation vapor pressure curve with respect to temperature [$Pa K^{-1}$]
- g_{ld} = leaf total conductance of water vapor (incl. stomatal and boundary layer) [$m s^{-1}$]
- $g_{HR} = g_{HR}(u, l_{leaf})$ = leaf boundary layer radiative and thermal conductance of heat [$m s^{-1}$] (Jones, 1992, p. 108)
- r_{sd}, r_{bd} = resistance to water vapor diffusion, stomatal and boundary layer [$s m^{-1}$]
- u = wind speed [$m s^{-1}$]
- l_{leaf} = leaf length scale [m]

Boundary layer conductance to heat transfer for a flat plat, g_{AH} , is given in Appendix D on Leaf Boundary Layer Conductances/Resistances.

The common assumption of plant ecophysiology modelers is that, at the time scales of most measurement methods, the leaf temperature achieves equilibrium with the ambient air temperature. The change in leaf temperature occurs at the scale of seconds in response to environmental fluctuations. At the half-hourly time scale, it may be assumed that the leaf is in equilibrium with the environment, so that $T_l = T_e$ (Su, et.al., 1996).

The equilibrium leaf temperature equation above makes the following assumptions:

1. The leaf temperature is at steady-state with respect to the air temperature.
2. The net radiation of the leaf is a function of the leaf temperature itself.
3. The slope of the saturation vapor pressure curve is constant between T_a and T_{leaf} .
4. Heat storage in the leaf is negligible (at equilibrium).

At this point, the basic budget equations have been laid out for leaf gas exchange: water vapor, carbon dioxide, and energy, with photosynthesis fully specified. In general, the earlier workers used less complex models of photosynthesis, since this was still a developing area of research, and they neglected boundary-layer and mesophyll resistances, either for the sake of simplicity or because these phenomena were not yet well-known. Those are more issues of implementation rather than of major conceptual changes. Cowan and Farquhar (1977) formed both budget equations for water vapor and CO_2 , assumed steady-state for CO_2 , and, utilized a model of photosynthesis by Hall (1971) (this was before the Farquhar and von Caemmerer 1982 model of photosynthesis had been fully formulated). The Finnish team used a Jarvis-type model for photosynthesis. Cowan and Farquhar (1977), Givnish (1986), and the Finns neglect boundary-layer resistances and do not address leaf tempera-

ture in their models for the sake of simplicity. Hari (1986) and Lloyd (1991) followed the work of Cowan and Farquhar, providing an analytical solution for g_s where the other two had not, based on very simple biochemical models of assimilation. Givnish (1986) adds the detail of relating assimilation rate to leaf water potential (which affects mesophyll resistance), and transpiration rate to root water uptake (linking these two with leaf water potential), such that both photosynthesis and transpiration are constrained by soil moisture. Friend (1995) utilized all three budget equations with the conventional assumptions, including boundary layer and mesophyll resistances. He used Farquhar and von Caemmerer's (1982) model of photosynthesis, and his overall formulation is the most solid in the biophysics and biometeorology and up-to-date in the biochemistry. Having laid out these leaf equations for unstressed conditions, optimality modeling is now addressed to account for drought.

4.2.3 Defining "available water" and "optimality"

The major conceptual difference among the above groups of optimality models is in how they performed the optimization, and it is here where the real pitfalls occur. Their optimality criteria are listed in Table 4.1 for non-drought situations and in Table 4.2 for drought situations. In examining these, the reader should note how they deal with the availability of water, if at all.

The listings of optimality criteria in Table 4.2 show how the theory has developed from a philosophical and purely theoretical formulation to increasing efforts at detail and accuracy. All are leaf-level models, with later attempts to incorporate the constraints of soil moisture availability. Friend's (1995) modeling of leaf water potential incorporates the

Non-drought situations:	
Cowan and Farquhar (1977), Cowan (1977)	$\underset{g_s}{\text{Minimize}} \int (E(t) - \overline{E}) dt$ subject to: $\int (A(t) - \overline{A}) dt = 0$ which gives: $\frac{\partial}{\partial g_s} \int (E(t) - \overline{E}) dt = \lambda \frac{\partial}{\partial g_s} \int (A(t) - \overline{A}) dt$ where: $\overline{A}$ and $\overline{E}$ are the average rates of assimilation and transpiration within a time period T. λ, Lagrange multiplier, is interpreted as the "cost of water" and solves to be: $\lambda = \frac{\partial E / \partial g}{\partial A / \partial g} = \frac{\partial E}{\partial A}$ (Note: This is a more precise presentation of λ than the original authors').
Givnish (1986)	$\underset{r_c, f}{\text{Maximize}} f \cdot A(r_c, f, \Psi_{leaf}, (VPD, k_{root}))$ where: r_{l,CO_2} = total leaf resistance to CO_x diffusion f = leaf allocation of assimilation to dry matter Ψ_{leaf} = leaf water potential VPD = vapor pressure deficit k_{root} = root hydraulic conductivity Constraint: soil water potential
Hari (1986), Lloyd (1991)	same as Cowan and Farquhar (1977), but with analytical solutions on different assimilation models

Table 4.1: Optimality criteria of various stomatal conductance optimality models.

Drought situations:	
Cowan (1986)	probability of surviving a drought period, where $\bar{A}$ and $\bar{E}$ are replaced by probabilistic counterparts (very vague derivation!)
Mäkelä (1996)	$\underset{g_s}{\text{Maximize}} \mathbb{E} \left\{ \int_0^T A(t) dt \right\} = \int_0^\infty e^{-kt} A(t) dt$ subject to: $\int_0^\infty E(t) dt \leq W_{s0}$ where: t = time k = probability of rain [d⁻¹] W_{s0} = available water at beginning of a drought period
Friend (1995)	maximize dry matter production: $W_d = f_{\Psi_{leaf}} \cdot k \cdot A$ with respect to r_{leaf} where: $f_{\Psi_{leaf}}$ = scaling function of leaf water potential k [kg m² mol⁻¹] = proportionality constant for allocation to dry matter

Table 4.2: Optimality criteria in various stomatal conductance models for drought.

most up-to-date parameterizations of plant biophysical characteristics and exogenous soil moisture.

It is important to note that the researchers do not all model the same kinds of expected plant behaviors, even in the case of non-drought situations. Cowan and Farquhar's (1977) optimality criteria describe vegetation behavior as minimizing departure from some mean transpiration and assimilation total, which could represent some adaptation to mean annual resources. Such a description for vegetation behavior may be realistic for some plants, since plants are not always more productive with an increase in a year's resources, but may finish their annual growth according to some sufficient level corresponding to, e.g. growing degree-days, or some amount of allocation to reproduction and storage. (Note that it was not so easy to re-phrase Cowan's optimality criteria formally mathematically, as he relied on much verbiage to squeeze it within the framework of Lagrange multipliers, so the presentation in Table 4.1 is more precise interpretation). By contrast, Givnish (1986), Hari (1986) and Lloyd (1991) model the plants as infinitely greedy, always increasing the immediate level of assimilation, given more water. For drought situations, Cowan (1986) replaces $\bar{A}$ and $\bar{E}$ with probabilistic expressions to represent the plant's expectation of resources. Mäkelä's (1996) utilizes the probability of rain, which serves as a discount function of the future, not dissimilar conceptually to Cowan (1986). Friend (1995) merely multiplies in a conventional Jarvis-like water stress factor, without any definition of that stress factor in terms of climate (although this could be possible).

Cowan and Farquhar's (1977) initiation of this line of research spun off efforts by other researchers puzzling over the meaning of the "cost of water," λ . Cowan and Farquhar's

theoretical explorations showed the solution of their optimality criterion to be an infinite surface relating g_s and λ . Given an infinite set of solutions, researchers had to ask, in reality, Should λ be constant? Over what time scales can we expect it to vary? etc. These questions continue to cause researchers puzzlement in trying to match observations to the theory (e.g. Thomas, et.al., 1999; Koskela, et.al., 1999). Givnish (1986) recognized the problem of the lack of a physical definition of λ , and, therefore, his optimality model avoids this problem by doing a strict maximization on assimilation, but note that this implies a different kind of plant adaptation. Givnish (1986) and Friend's (1995) optimality criteria, interestingly, do not directly optimize on water, which is a deterministic driver of the assimilation rate, rather than a budget constraint (soil moisture is exogenous to the model). Mäkelä (1996) described the same kind of plant adaptation as these two researchers, but does not avoid the λ problem, because in solving the problem using the Hamiltonian, another similar optimization parameter must still be introduced, p , which Mäkelä then fits to observed data. Mäkelä's model also has the shortcoming of being uncertain about how to define "available soil moisture," because that soil moisture availability is defined on a mass basis, rather than as water potential or some other intensive rather than extensive measure.

Let us revisit the optimality criteria again and ask what best describes plant adaptations to climate: Are plants infinitely greedy, or are they adapted to stay within some mean level of behavior? Do plants always maximize water use efficiency, or are there some times when they may be less efficient? Somehow, it seems that the answer to each question is some combination of both cases. Plants are constrained according to their evolutionary behavior, while they also respond to both interannual and daily (hourly, seconds) variation

in weather and may change in their annual productivity and leaf area. When plants are well-supplied with water, stomatal conductance is more likely to be constrained by assimilation rate than by water use, while stomatal closure is commonly observed in plants under water stress. Meanwhile, at the landscape scale, vegetation are observed to maximize use of available resources by maximizing cover or leaf area according to the mean annual climate. Obviously, the temporal course of water use efficiency of vegetation can be expected to vary, such that Cowan's λ is certainly not constant. *The conceptual difficulty lies in distinguishing simultaneous adaptive behaviors that are occurring: spatially at the leaf scale and at the landscape scale; temporally according to immediate environmental conditions, as well as seasonal cycles and long-term equilibrium.* Somehow, both the spatial and the temporal scales must be linked in order to formulate a truly coherent optimality model of stomatal conductance.

Let us now develop step-by-step the criteria for optimal water use, stated succinctly: maximize assimilation constrained by available water. The common way to express this would be to maximize water use efficiency (WUE), where "efficient" conventionally means benefit/cost, that is, A/E . Note that more refined definitions of WUE are possible – it is assumed here that A includes dark respiration, and therefore is net assimilation. This optimization via maximization of WUE can be quantified either with respect to immediate rates or as integrals over some finite period of time. If the case of unconstrained water supply is examined, the leaf WUE criteria can be stated mathematically:

No drought:

Immediate WUE:

$$\text{maximize } \frac{A}{E} \text{ with respect to } g_l \quad (4.19)$$

WUE over some time period $[0, T]$:

$$\text{maximize } \frac{\int_0^T A dt}{\int_0^T E dt} \text{ with respect to } g_l \quad (4.20)$$

One can see immediately that Lagrange multipliers are not needed to perform the optimization here, as simple differential calculus is adequate. Thus, differentiating the above expressions to obtain the extrema one obtains:

Immediate WUE:

$$\frac{\partial}{\partial g_l} \left(\frac{A}{E} \right) = 0 \quad (4.21a)$$

$$\text{Applying the differential: } \frac{\partial A / \partial g_l}{E} + \frac{A}{-E^2} \frac{\partial E}{\partial g_l} = 0 \quad (4.21b)$$

$$\text{and rearranging: } \frac{\left(\frac{1}{E} \frac{\partial E}{\partial g_l} \right)}{\left(\frac{1}{A} \frac{\partial A}{\partial g_l} \right)} = 1 \quad (4.21c)$$

WUE over some time period $[0, T]$, obtained in the same way:

$$\frac{\frac{1}{\int_0^T E dt} \left(\frac{\partial}{\partial g_l} \int_0^T E dt \right)}{\frac{1}{\int_0^T A dt} \left(\frac{\partial}{\partial g_l} \int_0^T A dt \right)} = 1 \quad (4.22a)$$

The final expression in both cases is an **elasticity**, which is a familiar dimensionless quantity found in all introductory microeconomics textbooks to quantify how markets adjust to changes in supply, demand, price, income, etc. Since the economics of water use efficiency are being discussed, it is a logical step to draw from a well-developed discipline that devotes

itself to calculating budgets and maximizing utilities (with the caveat that economists have violated laws of conservation in physics in their pursuit of unlimited growth; Mirowski, *More Heat Than Light*). The elasticity gives the relation between the percent change in one quantity versus the percent change in another quantity, where the two are interdependent. The elasticity here would be analogous to the price elasticity of demand, where the price is transpiration and assimilation is what is demanded (other analogies to income, supply, etc., are also possible, but it is not necessary to map the WUE elasticity one-to-one to particular cases in economics). An elasticity equal to 1 is termed “unit elasticity,” which implies that any percent increase in E (or A) must be accompanied by an equal percent increase in A (or E) (or their integrals, in the case of optimization over a time period). If the system deviates from this relation, then it is not behaving optimally. This relation is invariant, and there is no need to worry about Cowan and Farquhar’s λ . At the same time, this relation does not imply a constant λ , either, but, rather, Equation 4.21c implies that:

$$\lambda = \frac{\partial E / \partial g_l}{\partial A / \partial g_l} = \frac{E}{A} \quad (4.23)$$

Therefore, Cowan and Farquhar’s (1977) λ is merely a reflection of water use efficiency (or, rather, $1/\text{WUE}$), but that WUE must depend then on how g_s controls and is controlled by E and A . This answers the question of whether λ is constant. Observations show that E/A is often maintained nearly constant but also varies with environmental conditions due to plants’ ability to acclimate, and therefore λ must also vary (Thomas, et.al., 1999a,b). The solution for g_s , then, would be obtained in this particular optimality formulation by preserving the unit elasticity of assimilation with respect to transpiration. The question about whether λ varies concerns how much water use efficiency changes, while the question

of whether the plant has achieved its optimum water use efficiency is best answered by asking if the elasticity in Equation 4.21c departs from 1, as this is the real measure of how far away from the optimum the plant's water use efficiency is.

Note that when considering the problem of maximizing A/E with respect to all potential controllers, basic differential calculus requires that, if an extremum is truly obtained, then all the first-order partial derivatives must equal zero:

$$\frac{\partial(A/E)}{\partial g_l} = \frac{\partial(A/E)}{\partial VPD} = \frac{\partial(A/E)}{\partial T} = \frac{\partial(A/E)}{\partial PAR} = \frac{\partial(A/E)}{\partial \dots} = 0 \quad (4.24)$$

Thus, more elasticities as in Equation 4.23 follow. Thomas, et.al. (1999a,b) performed a thorough comparison of the partial derivatives of A and partial derivatives of E – but not of A/E – for several researchers' different models of E and A , examining their partials with respect to vapor pressure deficit, temperature, light, and interstitial CO_2 as well as stomatal conductance. Their aim was to see which representations were most practicable for calculating λ measured in the field and lab, and to see whether this ratio, the "cost of water," is constant with respect to the different drivers. Due to the nature of the equations chosen for E and A (from Cowan and Farquhar, 1977), the partial equations could not give them analytical insight into the roles of light and soil moisture. Therefore, in their data analyses, they regressed λ versus different drivers in lab leaf gas exchange measurements, and they observed this quantity varying with respect to light and soil moisture (leaf water potential) but not significantly varying with respect to temperature. It is not surprising that Thomas, et.al. (1999b) observed such variation, since the derivation above of the elasticity shows that there is no reason for λ to be constant over time or changing conditions if the plant is always adjusting to maximize water use efficiency – for the given conditions.

The above formulations tell whether or not a plant is maximizing WUE, but they do not explicitly express what is constraining WUE from its maximum (i.e. what is perturbing the elasticity away from 1). Let us explicitly impose that constraint with respect to soil moisture: by making general the case of drought. Now we enter into more philosophical territory, and here are some options on how to impose the constraint on transpiration:

Drought:

Immediate WUE:

$$\text{maximize } \frac{A}{E} \quad \text{with respect to } g_l \quad (4.25a)$$

$$\text{subject to } E \leq k_{plant} (\Psi_{leaf} - \Psi_{soil}) = E_{mesophyll} \quad (4.25b)$$

$$\text{where } k_{plant} = \text{hydraulic conductivity of the plant} \quad (4.25c)$$

WUE over time period $[0, T]$:

$$\text{maximize } \frac{\int_0^T A dt}{\int_0^T E dt} \quad \text{with respect to } g_l \quad (4.26)$$

$$\text{subject to } \int_0^T E dt \leq \text{available soil moisture} \quad (4.27)$$

In the case of optimizing immediate WUE, it would make sense that the transpiration rate E cannot exceed the immediate supply rate of water through the plant, as was noted in the leaf water vapor budget equation, Equation 4.7a. This constraint must be valid for non-droughted plants, as well. Such a criterion would require then a model of hydraulic conductivity of the plant and soil, such as that used by Givnish (1986); the complications in predicting the supply rate through the plant were discussed in Chapter 1, e.g. due to hormonal signals and the supply rate not being in steady-state with leaf transpiration due

to capacitance effects. The constraint cannot be posed to avoid the issue of plant hydraulic conductivity, since it is not clear what the upper limit on the supply rate should be when soil moisture is limiting. It is known that plants enhance evapotranspiration above the rate of soil evaporation (e.g from deforestation studies; Dickinson, 1989), and this enhancement is a function of the plant below- and above-ground architecture.

In fact, Cowan and Farquhar's (1977) statement of the problem actually is a variation of the setup in Equations 4.25abc. Referring again to their framework as stated in Table 4.1, one can see that $\bar{A}$ and $\bar{E}$ are constants representing some optimum levels for the time period T . In the limit as $T \rightarrow 0$ (T is, after all, arbitrarily specified) and applying the derivative with respect to g_s , $\bar{A}$ and $\bar{E}$ simply cancel out, which is equivalent to saying to maximize A with respect to g_s , subject to $E \leq \tilde{E}$, where $\tilde{E}$ is some immediate constraint on the rate of transpiration, akin to $\bar{E}$. This then gives $\partial A / \partial g_s = \lambda \partial E / \partial g_s$, giving Equation 4.23. This is not equivalent to maximizing A/E subject to a constraint, but it is equivalent to stating that the elasticity (Equation 4.21c from trying to maximize A/E) departs from 1. In which case, perhaps it might be useful to define a parameter, say ε for the elasticity, and notice that $\frac{\partial E / \partial g_s}{\partial A / \partial g_s} = \varepsilon \frac{E}{A} = \lambda$. At any rate, Cowan and Farquhar's (1977) model is mathematically equivalent to one that could be formulated specifying a water (or other resource) constraint. Their described constraint that the plant is seeking to stay close to an optimum level of A then could be equivalent to saying that adaptation to climate is the same thing as maximizing under a constrained resource. The λ is the measure of the water use efficiency of the plant, but the elasticity tells whether the plant is behaving optimally without restriction (and different WUE may be optimal for different conditions,

species, etc.). If the elasticity does not equal 1, then there is a departure from the optimum. These are two different kinds of optimality questions that must be distinguished. (So, Cowan and Farquhar's model in Table 4.1 could instead be placed in Table 4.2).

The above summarizes the kinds of optimality frameworks and criteria that have been used to date, showing the development and the various attempts to simultaneously account for plant responses to the immediate environment as well as strategies over time. Most appear to work not too badly, primarily because there is no controversy over the physics of diffusion, which accounts for the bulk of variation in stomatal conductance. The relations to soil moisture are still awkwardly formulated, the best being by Givnish (1986), which must still rely on the ill-defined hydraulic conductance of the plant. It is, of course, natural to want to pursue the idea of elasticities further, the way previous researchers have pursued their various optimality criteria, examining the sensitivities to different driving parameters, checking the ability of *these* criteria to mimick actual conductance measurements. Indeed, further examination will no doubt yield useful theoretical insights. However, these optimality criteria are ultimately still unsatisfactory, due to the way the time constraint is imposed: what is T ? One second? One hour? A day? A season? An entire year?

Ultimately, the fixed-time framework of these models and their focus on the leaf level limits them from being able to incorporate both the immediate physics and the probabilistic strategy of plant gas exchange and the specification of available soil moisture. What is needed to accomplish these simultaneous goals is another class of optimality theory: that of **stochastic optimal control**. In the next section, this class of problems is described, and it is shown how it is a means to solve the conceptual problems encountered by the

previous optimality models of leaf gas exchange response to drought.

Chapter 5

A new optimality model of stomatal conductance

5.1 Introduction to stochastic optimal control

The following general description of stochastic optimal control is taken from the book by Björk (1998), *Arbitrage Theory in Continuous Time*, generalized for event-driven processes, following Belavkin (1993). The idea is that, in trying to maximize some desired quantity given a certain amount of resources, the utilization of those resources must be steered in real time based on current conditions, given some future expectations, based on past experience. The amount of resources and the various processes that are adapted to those resources are subject to both deterministic and stochastic influences. In some sense, plants behave more rationally than consumers, since knowledge is universally broadcast to all through environmental conditions, so extending the old economic analogies for

plant resource use to modern-day finance models (however much it may violate our plant ecophysiological environmentalist aesthetics) is...inevitable!

More concretely in mathematical terms: **stochastic optimal control** problems involve a **state process** or **state variable**, X , which is subject to a **control process**, $\mathbf{u}$, that controls or "steers" both deterministic and stochastic influences on X . These processes and controls can be vectors to represent multiple components, $\mathbf{X}$ and $\mathbf{u}$. Optimization involves maximizing over time a **value function**, $\mathcal{J}$, which is the expected value of the time integral of an **instantaneous value function**, F , of the state variable and finding solutions for the control process. The solution gives the **optimal control law**, $\hat{\mathbf{u}}$. The solution method requires dynamic programming, which involves calculating expected values within time increments, taking the limit as the time difference goes to zero. Thus, the optimization is performed over time, but dynamically and not statically. For a more rigorous presentation of dynamic programming, the reader should consult Björk (1998).

So, the general **control problem** is defined as the problem to maximize the expected value of the time integral of the value function:

$$\mathcal{J}(t, x, \mathbf{u}) = E_{t,x} \left\{ \int_t^T F(s, X_s^{\mathbf{u}}, \mathbf{u}_s) ds + \Phi(X_T^{\mathbf{u}}) \right\} \quad (5.1)$$

given certain dynamics of $\mathbf{X} \in R^n$ and constraints on $\mathbf{u}$. Here, lower-case $t \in R_+$ and $x \in R^n$ denote fixed points, and $\mathbf{u}$ in this case is adapted to the state process X , such that $\mathbf{u}_t = \mathbf{u}(t, X_t) \in R^k$. Φ is a "legacy" function, which measures the utility of having some resources left over at the end of the period $[t, T]$.

The time dynamics of X are expressed in a **controlled** stochastic differential equa-

tion (SDE):

$$dX_t = \mu(t, X_t, \mathbf{u}(t, X_t)) dt + \sigma(t, X_t, \mathbf{u}(t, X_t)) dW_t + \xi(t, X_t, \mathbf{u}(t, X_t)) dY_t \quad (5.2)$$

$$X_t = x \quad (5.3)$$

where $\mu(t, X_t, \mathbf{u}(t, X_t)) \in R^n$ is a deterministic influence, $W \in R^n$ is a Wiener process whose variance is scaled by $\sigma(t, X_t, \mathbf{u}(t, X_t)) \in R^{n \times d}$ at time t , and $Y \in R^n$ is a Poisson process marked by a magnitude $\xi(t) \in R^{n \times d}$ that may also be a random variable. The Wiener process represents random drift in X , with value zero at $t=0$, and the marked-Poisson process describes the occurrence of random events.

The problem has the constraints:

$$\mathbf{u}(s, y) \in \mathcal{U}, \forall (s, y) \in [t, T \times R^n] \quad (5.4)$$

where $\mathcal{U}$ is the class of admissible controls laws, which requires that for any given initial point (t, x) , the above SDE has a unique solution. (Note that s, y are used for the variables, since t and x denote the fixed points).

Finding the optimal control law, $\hat{\mathbf{u}}$, that gives a maximum objective $\mathcal{J}$ is done dynamically by finding a control law $\mathbf{u}$ that satisfies the Hamilton-Jacobi-Bellman (HJB) equation. The details HJB equation are given in Appendix J.

5.2 Stochastic optimal control of soil moisture

Given this general framework of stochastic optimal control, the problem of stomatal conductance under drought may then be expressed as having the state variable vector of environmental drivers and soil moisture, with the plants maximizing assimilation at the

canopy or landscape scale, A_{veg} , over time, with their controls being leaf stomatal resistance, r_s , photosynthetic capacity, $V_{c\max}$, and leaf area index, LAI , and with the soil moisture dynamics and plant activity subject to exogenous, stochastic environmental processes. The soil moisture dynamics are an SDE that describes the change in soil moisture due to plant transpiration, E_{veg} , soil evaporation, E_{soil} , infiltration from rain, R , and losses due to runoff, Q , and leakage, L . The environmental drivers are also SDE's that are just functions of time.

5.2.1 The control problem

The basic components of the control problem are as follows:

$$\text{state process : } \mathbf{X}(t, \mathbf{X}_t, \mathbf{u}_t) = \begin{pmatrix} T_a(t) \\ RH(t) \\ PAR(t) \\ u(t) \\ c_a(t) \\ S(t, \mathbf{X}_t, \mathbf{u}_t) \end{pmatrix} \quad (5.5a)$$

$$\text{control process : } \mathbf{u}(t, \mathbf{X}_t) = \begin{pmatrix} r_s(t, \mathbf{X}_t) \\ LAI(t, \mathbf{X}_t) \\ V_{c\max}(t, \mathbf{X}_t) \end{pmatrix} \quad (5.5b)$$

$$\text{instantaneous value function : } F = A_{veg}(t, \mathbf{X}_t, \mathbf{u}_t) \quad (5.5c)$$

$$\text{legacy function : } \Phi = 0 \quad (5.5d)$$

where S is soil moisture in meters, which can be normalized to $s = S/(nZ_r)$, where n is soil porosity, Z_r is soil depth. T_a , RH , PAR , u and c_a are environmental drivers, air temperature, relative humidity, photosynthetically active radiation, wind speed, and ambient CO₂ concentration, respectively. Notice that the environmental drivers are simply functions of time, as they are considered exogenous to vegetation. Of course, there exist feedbacks between vegetation and air temperature, humidity, and ambient CO₂ concentration, but these feedbacks must be the subject of other investigations than that here. Soil moisture, S , on the other hand, is also a function of the state process vector and the vegetation controls.

Vegetation has three controls in the control process, $\mathbf{u} = \langle r_s, V_{c\max}, LAI \rangle$:

$r_s(t, X_t) = \text{leaf stomatal resistance to water vapor diffusion } [\text{mol}^{-1} \text{ m}^2 \text{ s}^1]$

$LAI(t, X_t) = \text{leaf area index}$

$V_{c\max}(t, X_t) = \text{photosynthetic capacity } [\text{mol m}^{-2} \text{ s}^{-1}]$

Note again that r_s and $V_{c\max}$ are leaf-level parameters, LAI is a total-landscape (per area) parameter, and that scaling up leaf transpiration by LAI gives landscape-level transpiration and assimilation. Thus r_s and LAI are both controls on soil moisture, S , but the first two at the leaf scale and the latter at the landscape scale, both linked through S .

The assumption can be made that the vegetation gains no benefit from having un-utilized water at the end of the growing season.

Constraints

The differential constraint is a vector of the SDE's of the environmental variables and soil moisture dynamics, with an integral constraint for the boundary condition. Note that stochastically-driven variables must be expressed as a stochastic differential, dX^{stoch} , whereas deterministic variables are expressed in terms of time increments, $X^{det}dt$.

controlled SDE:

$$dX_t = \mu(t, X_t, \mathbf{u}_t) dt + \sigma(t, X_t, \mathbf{u}(t, X_t)) dW_t + \xi(t, X_t, \mathbf{u}(t, X_t)) dY \quad (5.6a)$$

$$= \begin{pmatrix} dT_a(t) \\ dRH(t) \\ dPAR(t) \\ du(t) \\ dc_a(t) \\ dS_t(t, \mathbf{X}_t, \mathbf{u}_t) \end{pmatrix} \quad (5.6b)$$

where μ is an n -dimensional vector, σ is an $n \times k$ matrix, dW is a k -vector of Wiener processes, η is an $n \times l$ matrix, ξ is a diagonal matrix of random variables to mark the magnitudes of the elements of dY , which is an l -vector of Poisson processes. These variables, of course, are not necessarily independent of each other, such that the matrices for σ and η may contain non-zero covariances, for example for temperature, T_a , and relative humidity, RH . The individual equations for the state variables are described in the sections below.

Objective function

The objective is to maximize the expected amount of carbon assimilation at the

canopy or landscape scale, given a time horizon, $\mathcal{T}$, that marks the start of a new seasonal cycle. The **value function**, $\mathcal{J}(t, \mathbf{X}_t, \mathbf{u}_t)$ can be defined as:

$$\mathcal{J}(t, \mathbf{X}_t, \mathbf{u}_t) = E_{t, \mathbf{u}_t} \left\{ \int_t^{\mathcal{T}} A_{veg}(t, \mathbf{X}_t, \mathbf{u}_t) d\tau \right\} \quad (5.7)$$

and the objective is to maximize $\mathcal{J}$. Thus, at time t , the vegetation maximizes its assimilation of carbon based on its statistical expectation of future environmental conditions, subject to the current soil moisture constraints. Note that this finite time constraint works only for a system with pronounced seasonal cycles and annual water deficits. For systems that are continuously productive, it would be more appropriate to have an indefinite time integral, with a discount function that discounts the importance of the future; however, the form and magnitude of this discount function would have to be determined.

The dynamics of the individual exogenous climate drivers and the endogenous plant and soil processes are given below. In the notation, the specific environmental drivers and vegetation controls for each process will be explicitly identified to enable the reader to distinguish which variables are significant to each process.

5.2.2 Exogenous environmental drivers

The environmental drivers, air temperature, T_a , relative humidity, RH , photosynthetically active radiation, PAR , wind speed, u , and ambient CO_2 , c_a , are all stochastic variables derived from climate statistics, which may be modeled as incorporating Wiener processes for their stochasticity, such that there is no Poisson component for these drivers. They are considered here as functions only of time, exogenous to vegetation controls. Below are examples of how they might be possibly modeled from historical climate data (these

examples are not set in stone, but are illustrative of how their deterministic and stochastic components could be represented).

- **Air temperature**, T_a , may be modeled as a sine curve with a stochastic part that is Gaussian in distribution, where B is the amplitude in the the diurnal variation, changing over the course of the year, ω is the frequency of the diurnal variation, σ is the standard deviation for the Gaussian random variation.

$$dT_a = B_{T_a,day} \sin(\omega_{T_a,day} t) dt + B_{T_a,year} \sin(\omega_{T_a,year} t) dt + \sigma_{T_a} dW(T_a) \quad (5.8a)$$

$$\overline{T_a} |_{year} = \overline{T_a} \quad (5.8b)$$

More complex modeling can be done to account changes in the mean and other seasonal variations, with parameters fit to historical climate data.

- **Relative humidity**, RH , may be modeled similarly to air temperature:

$$RH : dRH = B_{RH,day} \sin(\omega_{RH,day} t) dt + B_{RH,year} \sin(\omega_{RH,year} t) dt + \sigma_{RH} dW_{RH} \quad (5.9a)$$

$$\overline{RH} |_{year} = \overline{RH} \quad (5.10)$$

- **Wind speed**, u , within canopies does not have a general simple form (Grace, 1977; Raupach and Shaw, 1982; Rodean, 1996). For an open canopy, a mean wind speed with diurnal cycles may be considerate adequate for purposes here.
- **Photosynthetically active radiation**, PAR , may be approximated as a sine curve with a stochastic part, $d\Theta$, representing reduction of radiation by clouds (distribution

not yet known, complicated):

$$dPAR = B_{PAR,day} \sin(\omega_{PAR,day}t)dt + B_{PAR,year} \sin(\omega_{PAR,year}t)dt - d\Theta_{PAR} \quad (5.11a)$$

$$\overline{PAR}|_{year} = \overline{PAR} \quad (5.11b)$$

- **Infiltration from rainfall**, R , is rainfall minus interception by the plant canopy and is a marked Poisson process. R is a function of three components: rainfall depth, H , an exponential random variable with mean α [m]; occurrence of rainfall, e , a Poisson process with mean time between events λ_R [d⁻¹]; and leaf area index, LAI , which determines infiltration (Laio, et.al., 2001a).

$$\text{rainfall minus interception, } R \text{ [m]} : dR(\lambda_R, \alpha, LAI) = Hde \quad (5.12)$$

$$\text{rainfall depth, } H \text{ [m]} : f_H(h) = \frac{1}{\alpha} \exp\left(-\frac{1}{\alpha}h\right) \text{ for } h \geq 0 \quad (5.13)$$

$$\text{rainfall occurrence, } e \text{ [indicator]} : \quad (5.14)$$

$$de = \left\{ \begin{array}{l} 1 \text{ with probability } \lambda_R dt + o(dt) \\ 0 \text{ with probability } (1 - \lambda_R) dt + o(dt) \end{array} \right\} \quad (5.15)$$

LAI imposes a threshold of rainfall depth, Δ , which reduces how much rainfall reaches the ground. For an open canopy, rainfall will always fall on open areas, with a fraction intercepted by the tree canopy, which effectively reduces the mean rainfall depth, giving shifted mean for the exponential rainfall depth, so that H can be replaced with H' :

$$\begin{aligned} \text{rainfall depth minus interception, } H' &= f_{H'}(h) \\ &= \frac{1}{\alpha - \Delta} \exp\left(-\frac{1}{\alpha - \Delta}h\right) \text{ for } h \geq 0 \end{aligned} \quad (5.16)$$

5.2.3 Vegetation processes

- **Vegetation transpiration**, E_{veg} , is due to both diffusion through the stomates and cuticular transpiration at the leaf level, scaled up by LAI (y is a spatial variable). This scaling up ideally requires a canopy model to account for the variation in environmental conditions throughout the canopy, but in an open system with fairly low leaf area index (not greater than 1), it should suffice to treat the canopy as a "big leaf", though the model could also be formulated using a canopy model to differentiate sun and shaded leaves (dePury and Farquhar, 1997):

$$E_{veg}(t, \langle S_t, T_{a,t}, RH_t, u_t \rangle, \mathbf{u}_t) \quad (5.17)$$

$$= \int_{space} E_{leaf}(y, \langle T_{a,t}, RH_t \rangle, \langle r_s(t, S_t) \rangle) \cdot LAI(y) dy \quad (5.18)$$

$$\approx E_{leaf} \cdot LAI, \text{ open canopy} \quad (5.19)$$

Equation 4.8 for E_{leaf} is substituted in to obtain the full expression with driving environmental variables.

- **Vegetation leaf surface evaporation**, $E_{vegsurf}$, can be represented as a bulk aerodynamic representation:

$$E_{vegsurf} = \frac{\rho_a}{r_b} (RH_{veg} w_{sat}(T_{leaf}) - w_a) \quad (5.20)$$

where ρ_a is air density, and RH_{veg} is relative humidity at the leaf surface.

- **Assimilation rate**, A , is modeled using the Farquhar-von Caemmerer (1982) model of photosynthesis at the leaf scale, A_{leaf} (control processes r_s and V_{cmax}), then scaled up by leaf area to the landscape scale (control process LAI), to give canopy-scale

assimilation, A_{veg} . Again, the "big-leaf" scaling is justified for the case of an open canopy, but alternative canopy formulations are also possible.

$$A_{veg}(t, \langle S, c_a, c_i, T_a, PAR \rangle, \langle r_s, V_{c\max}, LAI \rangle) \quad (5.21)$$

$$= \int_{space} A_{leaf}(y, \langle c_a, c_i(t, r_s(t, S_t)), T_a, PAR \rangle, \langle r_s(t, S_t), V_{c\max}(t, S_t) \rangle) \cdot LAI(y) dy \quad (5.22)$$

$$\approx A_{leaf} \cdot LAI, \text{ open canopy} \quad (5.23)$$

For A_{leaf} , the expressions for assimilation by biochemistry of photosynthesis, A_b , are substituted in, as given in Section 4.2.2, in Equation 4.15c, and in Appendix C, Equation C.5.

5.2.4 Soil hydrological processes

The soil moisture dynamics involve the change in soil moisture due to plant transpiration, E_{veg} , soil evaporation, E_{soil} , infiltration from rain, R , and losses due to run-off, Q , and leakage, L . R is a stochastic random variable as will be described later, whereas the other variables are all deterministic functions of the given stochastic environmental conditions.

$$dS_t = -E_{veg}(t, \mathbf{X}_t, \mathbf{u}_t) dt - E_{soil}(t, \mathbf{X}_t, \mathbf{u}_t) dt - (Q(t, S_t) + L(t, S_t)) dt + dR(t, \mathbf{X}_t, \mathbf{u}_t) \quad (5.24)$$

$$\text{boundary conditions : } S_0 = s_0 \quad (5.25)$$

$$S_t > S_h \quad \forall t \quad (5.26)$$

where S_h is the hygroscopic point of the soil moisture. Vegetation cannot extract soil moisture below the wilting point $S_w \geq S_h$.

- **Soil evaporation**, E_{soil} , is a function of soil moisture, climate drivers, and LAI.

The LAI influences how much the ground is sheltered, $shelt(LAI)$, by the vegetation (Noilhan and Planton, 1989; see observations on contributions of soil evaporation to total evapotranspiration in Jones, 1992, p. 123). One possible representation of soil evaporation is via a bulk aerodynamic representation (Noilhan and Planton, 1989; Mahfouf and Noilhan, 1991):

$$E_{soil}(t, \langle S_t, T_{a,t}, RH_t, u_t \rangle, LAI) = (1 - shelt(LAI)) \frac{\rho_a}{r_{soil} + r_a(u_t)} (RH_{soil,t} w_{sat}(T_{soil,t}) - w_a) \quad (5.27)$$

where:

$$RH_{soil} = \text{relative humidity in the soil pores} = \exp(\mathbf{g}\Psi_{soil}/(RT_{soil})) \quad (5.28)$$

$$r_{soil} = \text{soil resistance to water diffusion [m s}^{-1}\text{]}, \text{ function of } s_{surface} \quad (5.29)$$

$$r_a = \text{aerodynamic resistance above the soil} = (C_E u_a)^{-1} \quad (5.30)$$

where $\mathbf{g}$ is the gravitational constant, $9.81 \text{ [m s}^{-2}\text{]}$, C_E is the drag coefficient for evaporation (dependent on the thermal stability of the lower atmosphere), and $u_a \text{ [m}$

$s^{-1}]$ is the wind speed at an atmospheric reference level (e.g. 2 m). For r_{soil} there are a variety of empirical formulations that are functions of $s_{surface}$ (see Noilhan and Planton, 1989).

- **Run-off rate, Q** , is deterministic and can be modeled simply as an infinite rate when the soil is above its saturation point:

$$Q(t, S_t) = \text{infinite rate for } s_t = \frac{S_t}{nZ_r} = 1 \quad (5.31)$$

- **Leakage loss, L** , is deterministic and decays exponentially between soil at saturation, $s = 1$, and soil at field capacity,

$$s = s_{fc}L(t, S_t) = \frac{K_s}{e^{\beta(s-s_{fc})} - 1} \left(e^{\beta(s-s_{fc})} - 1 \right) \quad (5.32)$$

5.2.5 Solving the control problem via the HJB equation

The method for solving this problem involves finding an optimal control law $\hat{u} = \langle \hat{r}_s, \hat{V}_{c\max}, \widehat{LAI} \rangle$, such that $\mathcal{J}(t, \mathbf{X}_t, \langle \hat{r}_s, \hat{V}_{c\max}, \widehat{LAI} \rangle)$ is the optimal value function, $V(t, \mathbf{X}_t)$, the supremum of all possible $\mathcal{J}$:

$$V(t, \mathbf{X}_t) = \sup_{\mathbf{u} \in \mathcal{U}} \mathcal{J}(t, \mathbf{X}_t, \langle r_s, V_{c\max}, LAI \rangle) \quad (5.33)$$

$$= \mathcal{J}\left(t, \mathbf{X}_t, \langle \hat{r}_s, \hat{V}_{c\max}, \widehat{LAI} \rangle\right) \quad (5.34)$$

For $V(t, \mathbf{X}_t)$ to be the optimal value function, the necessary and sufficient condition is that V satisfies the Hamilton-Jacobi-Bellman equation, which is detailed in Appendix J:

$$\frac{\partial V}{\partial t}(t, \mathbf{X}_t) + \sup_{\mathbf{u} \in \mathcal{U}} \left\{ A_{veg}(t, \mathbf{X}_t, \langle r_s, V_{c\max}, LAI \rangle) + \mathcal{D}^{\langle r_s, V_{c\max}, LAI \rangle}(V(t, \mathbf{X}_t)) \right\} = 0 \quad (5.35)$$

$$\forall (t, \mathbf{X}_t) \in (0, T) \times \mathcal{R} \quad (5.36)$$

where $\mathcal{D}^{\mathbf{u}}$ is the partial differential operator for stochastic differential equations, or Dynkin operator, as given in Appendix J.

Solving the non-linear partial differential equation Equation 5.35 requires dynamic programming. Dynamic program typically involves making an educated guess about the form of V with a finite number of parameters and using Eq. 5.35 to identify the parameters. Because of the complexity of the numerous driving variables and processes, the solution is left to a future mathematician.

The problem of optimal stomatal control has been presented here in its most thorough and general form. The setup here is suitable for solving for temporal variation in the vegetation's controls, $r_s, V_{c\max}, LAI$, given genetic constraints, such as rooting depth or leaf size. This suite of parameters then will form a family of solutions – of potential vegetation of different possible strategies that are capable of optimizing resource use in the landscape. Recognizing that specifying optimality of stomatal control requires the top-down constraint at the landscape scale, this stochastic optimal control formulation offers the framework to allow the tying together of leaf (gas exchange) and landscape (resource limitation) spatial scales, and the short (meteorological conditions) and long-term (adaptations to climate) time scales. Is such a model practical for the purpose of predicting hourly-scale gas exchanges at the stand scale? If it can provide the mean temporal dynamics of V_{Cmax} and LAI for a given climate and specified rooting depth and leaf size, then such computation can save much in field measurement time for parameterizing biogeographical models. Ultimately, whereas previous optimality models addresses only partial aspects of the problem, this model of stochastic optimal control fleshes out the full suite of temporal, spatial, and

functional specifications that must be addressed in an encompassing optimality model of stomatal control in water-stressed ecosystems.

Chapter 6

Closing

The question of optimality of vegetation water useage in water-limited ecosystems has been approached here from the angles of continuous biometeorological field budgets, hydrologists' probabilistic soil water balance, and ecophysiolgists' leaf gas exchange models, focusing on savanna ecosystems for their characteristic seasonal drought and water-limited woody canopy cover. The analytical approach has been favored here over the simulations of climatologists in order to focus on theoretical relations.

In field measurements at the Ione, California, blue oak savanna, the first, well-rounded useage of biometeorological techniques was done to partition continuously over seasonal cycles the evapotranspiration of the tree and understory layers in a heterogeneous ecosystem. The data set from a continuous year of measurements provides details on the fluxes of water vapor and energy, the plant physiological status, and the meteorological drivers over the seasons; continued measurements will eventually provide long-term measurements to analyze the role of interannual climate variability. With the 2001 data, soil

moisture critical points were discerned in the transpiration rates of the oaks. While the two different vegetation growth forms, grass and tree, are phenomenologically known to be out-of-phase in their growing seasons, their seasonal trade off in the utilization of resources was quantified, from the energy-limited (and possibly nutrient or grazing-limited, next research) winter growth of the drought-avoiding annual grasses, to the water-limited summer of the drought-tolerant blue oaks. The grasses in winter achieve an actual evapotranspiration that tracks potential evapotranspiration but is still limited below potential values, and the blue oaks in summer, through biochemical drought tolerance mechanisms, are able to prolong the utilization of soil moisture, exhibiting a steady linear decline over the summer, rather than exponential, as with the sparse pines. Each functional type has known physiological limits during their respective periods of dormancy (winter embolism in the oaks, summer loss of stomatal control or soil moisture access in the grasses, evergreen pines that can maintain transpiration in the winter but have low productivity in the spring and summer). These are details that explain in hindsight why each form has its respective season, but why they coexist at all requires further inquiry. Their out-of-phase growth periods and brief synchrony in the spring suggest some kind of seasonal coordination in the utilization of water and energy. This coordination perhaps support the theoretical finding of Enquist, et.al. (1998) and Enquist (2002) that the total energy use or productivity of plants in an ecosystem depends only on the rate of the limiting resource supply and not the plant form (although Liebig's Law of the Minimum may not always hold at the scale of an individual plant, perhaps this paradigm is supported at the scale of a whole ecosystem). In other words, the seasonal climate selects for different functional type, but the functional

types are suited to the overall system optimal utilization of resources as constrained by supply rate. This assumes, of course, that long-term evolution and equilibrium have been achieved in an ecosystem. What are then the basic functional aspects of the vegetation that demarcate their seasonal transition?

For hydrologists like Rodriguez-Iturbe and co-workers (2001), the basic functional aspects of vegetation are their rooting depth, a "maximum" transpiration rate, and critical soil moisture points at which the vegetation experience water stress and hence decline in their transpiration rate. In applying their probabilistic model of soil moisture balance to the Ione savanna, the measures of seasonal water stress for the grasses and the trees shows that average stress for each type is lower in its dominant season than for the other functional type. However, the distinction of seasonal periods is highly dependent on a climate parameter neglected by this hydrologists model: whereas their characterization of climate is solely by precipitation patterns, energy supply is necessary to distinguish the seasons appropriately to obtain a satisfactory interpretation of the tree and grass coexistence from the stress indicators. Also, the "maximum" transpiration rate of the vegetation hides the role of energy and leaf area, such that this parameter is not a fundamental quantity on its own. As a soil moisture balance mean predictor, the model is surprisingly accurate, but the vegetation parameterization requires refinement from first principles.

For ecophysiologists, the basic vegetation functional aspects happen at the scale of leaf-level processes of gas exchange: photosynthesis and transpiration. However, optimality models of water use by plant ecophysiologists have struggled with definition of the most critical aspect of the optimality, which is the constraining resource (Cowan, 1977; Cowan

and Farquhar, 1977; Hari, et.al., 1986; Mäkelä, et.al., 1996; Lloyd, 1991). Those who did address this issue rely on a water budget at the plant level alone and then require that elusive parameter, the plant hydraulic resistance (Givnish, 1986; Friend, 1995). Cowan (1977) does discuss the role of competition. The point now emphasized is that the optimality constraint in the water limited ecosystem must be specified at the spatial scale at which the constraint occurs: at the landscape scale. Ultimately, a complete model of optimal stomatal control – if it is to be a model that predicts short-term stomatal conductance (leaf processes) constrained by water availability (landscape), and if it is to avoid the unknown mechanisms of abscisic acid and the tortuous details of the stem transport pathway – requires a different kind of mathematical framework.

The stochastic optimal control model proposed here satisfies these requirements, as it provides a framework for predicting short-term (hourly) stomatal conductance in response to immediate environmental conditions, with water availability constrained at the landscape scale. Because the unknown mechanism that links the leaf response to soil moisture (abscisic acid, hydraulic pathway) cannot be invoked, an optimality criterion is relied on: that stomatal control is based also on the plant's expectations of future water availability. The model combines hydrologists' stochastic modeling of climate, plant ecophysiolgists' current knowledge of photosynthesis, and the fundamental biophysics of leaf gas exchange. The fundamental parameters of vegetation with respect to exchanges with the atmosphere are then these: stomatal conductance, photosynthetic capacity ($V_{C\max}$, the carboxylation capacity of Rubisco), leaf area index, maximum rooting depth, and leaf dimension. These are listed in order of the time scale of their temporal variation, with stomatal conductance being

the most rapidly varying (scale of minutes), photosynthetic capacity and leaf area varying seasonally, and rooting depth and leaf dimension being genetically determined (long-term time scale) (one may note that rooting depth may vary seasonally in some plants, hence the emphasis on the maximum rooting extent). The model predicts not only stomatal conductance, but also the two seasonally changing parameters. Because no one single functional mixture is the only one possible in any climate, genetically-determined parameters, rooting depth and leaf dimension, are specified exogenously, such that a family of solutions for a particular climate-soil system is possible. The solution of the model requires future work, but in its present form, it addresses the incompleteness of past optimality models of stomatal conductance and provokes further questions about the meaning of vegetation-climate optimality with respect to the fundamental leaf and soil processes now known.

6.1 Future research

This optimal control model is not the ultimate word, of course, on models of stomatal conductance under drought: some day if the mechanism for abscisic acid is uncovered, scientists may be able to model stomatal control entirely mechanistically. Also, an optimality model based solely on climate is not the ultimate word, of course, on what structures savanna ecosystems. Detailed simulation models exist that address the complex of interplay of nutrients and water competition in tree-grass dynamics (Belsky, 1990, 1994a, 1994b; Menaut, et.al., 1990; Jeltsch, et. al. 1996), the role of herbivory in these highly productive ecosystems (Coughenour, et.al., 1990; Ludwig, et.al., 2001), and the role of fire (Menaut, et.al., 1990; Hoffman, 1999), all of these being defining aspects of savannas as

much as climate. Future development of the optimality model (as long as the mechanisms are unknown) should seek ways to predict leaf dimension and rooting depth, currently exogenous inputs to the model, based on a climate parameters and soil-vegetation-atmosphere processes. Nutrients as a limiting resource should also be included with soil moisture, drawing upon the field of soil science to account for soil chemical as well as physical properties also having potential equilibrium levels (Jenny, 1941). The trajectory of mutual vegetation and soil development through time should also be addressed to explain the non-equilibril state of many ecosystems.

Overall, however, climate still is the broadest controller of the geographic distribution and structure of ecosystems, and clarifying its still uncertain role for the tree-grass coexistence in savannas may help simplify future ecological investigations. Because savannas occur at the intersection between humid and arid, woody and herbaceous, stable and unstable structure, this complex ecosystem necessarily forges links among disciplines: hydrologists, ecophysiologists, biometeorologists, climatologists. Because of these linkages, savannas may hold the key to making more precise Cowan's (1977) speculation that water use efficiency is "a plant physiological parameter fashioned by evolution in the context of an environment having certain statistical properties."

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Appendix A

Symbols

In the table of symbols below, '-' indicates that the value is not a constant, values in parentheses () are empirical values, and plain values are physical constants. The subscript x is a dummy subscript to indicate that the variable is modified by other subscripts.

Symbol	Name	Units	Value
a	ratio of diffusivities of H ₂ O vapor and CO ₂ in air	mm ² s ⁻¹ H ₂ O / mm ² s ⁻¹ CO ₂	1.6
A	assimilation rate of CO ₂ , subscripts: b -leaf biochemical, d -leaf diffusion, veg -vegetation canopy	mol m ⁻² s ⁻¹	-
$\bar{A}$	Cowan and Farquhar (1977) mean assimilation rate	mol m ⁻² s ⁻¹	
B	amplitude in sinusoidal model of some meteorological variables, subscripts: variable symbol		
$\mathbf{c}$	scaling constant in temperature-dependency expressions for photosynthetic parameters		
c	CO ₂ mole fraction, subscripts: a -ambient air, i -leaf intercellular space, s -leaf surface	ppm	
C	CO ₂ concentration, subscripts: a -ambient air, i -leaf intercellular space, s -leaf surface	mol m ⁻³	
C_{H_2O}	tree water capacitance	m ³ MPa ⁻¹	
C_{rel,H_2O}	tree water capacitance in terms of relative water content	MPa ⁻¹	
c_p	specific heat capacity, subscripts: a -air, 1012; l -leaf	J kg ⁻¹ K ⁻¹	
D_i	diffusion coefficient of a gaseous species	m ² s ⁻¹	
e	Poisson random variable of a rainfall event with mean λ	indicator	
e_{sat}	saturated water vapor pressure	Pa	
E	leaf transpiration rate	mol m ⁻² s ⁻¹	
E_x	evapotranspiration rate, subscripts: $cuticle$ -leaf cuticular, $leaf$ -leaf, $soil$ -soil, veg -vegetation canopy, $canopy$ -tree canopy	m s ⁻¹	
$\bar{E}$	Cowan and Farquhar (1977) mean leaf transpiration rate	mol m ⁻² s ⁻¹	
$E_{t,x}$	Expected value at time t and instance x of X in a control problem		

Table A.1: Symbols

f	Givinish (1986) leaf allocation of assimilation to dry matter	fraction	
F	value function in a control problem		
g_x , pressure-driven	leaf conductance of water vapor for pressure driving force, subscripts:	$\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$	
	0-Ball-Berry equation intercept, b -boundary layer, max-Jarvis maximum, s -stomatal,		-
	l -total leaf (incl. stomatal and boundary layer)		
g_0	Ball-Berry equation intercept	$\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$	$(8 - 80 \times 10^{-6})$
g_{xd} , concentration-driven	leaf-level conductance of water vapor diffusion for concentration driving force, subscripts:	m s^{-1}	
	bd -boundary layer, ld -total leaf (incl. stomatal and boundary layer), sd -stomatal		
g_{HR}	leaf-level boundary layer radiative and thermal conductance of heat	m s^{-1}	
G_x	canopy-level conductance, subscripts: aM - momentum; c -canopy water vapor; H -heat	m s^{-1}	
$\mathcal{G}_{soil}$	soil heat storage or loss by conduction	W m^{-2}	
h	instance of rainfall depth variable H	m	
$\mathcal{H}$	partial differential operator in control problem		
H	exponential random variable of rainfall depth, with mean α	m	
ΔH_a	activation energy in chemical temperature dependence	kJ mol^{-1}	
ΔH_d	deactivation energy in temperature-dependence of photosynthetic parameters		
I	irradiance	W m^{-2}	
$\mathcal{J}$	value function in control problem		
J	rate of electron transport	$\text{mol photon m}^{-2} \text{ s}^{-1}$	

$J_{\max}$	maximum rate of electron transport	mol photon $\text{m}^{-2} \text{s}^{-1}$	
k_g	Ball-Berry sensitivity of stomatal conductance to soil water content	fraction	
k_{root}	Givnish (1986) root hydraulic conductivity	$\frac{\text{g H}_2\text{O}}{\text{g}^{-1} \text{root MPa}^{-1} \text{s}^{-1}}$	
K_x	Michaelis constants, subscripts: <i>c</i> - carboxylation, <i>o</i> - oxygenation	ppm	
l	leaf length dimensions, subscripts: <i>i</i> -internal space thickness, <i>leaf</i> -mean length	[m]	
LAI	leaf area index		
m	slope of the Ball-Berry stomatal conductance equation	dimensionless	(6.9 – 10)
n	soil porosity	fraction	
o	O ₂ concentration in leaf intercellular air space	ppm	
P	barometric pressure	Pa	
P_v	water vapor partial pressure, subscripts: <i>a</i> -ambient air, <i>l</i> , <i>leaf</i> -leaf, <i>sat</i> -saturated	Pa	
PAR	photosynthetically active radiation	$\frac{\text{mol}}{\text{s}^{-1}}, \frac{\text{W}}{\text{m}^{-2}}$	-
$PPFD$	photosynthetic photon flux density	$\frac{\text{mol}}{\text{s}^{-1}} \text{m}^{-2}$	
r_x , pressure-driven	leaf-level water vapor diffusion resistance for pressure driving force, subscripts:	$\text{mol}^{-1} \text{m}^2 \text{s}^{-1}$	
	b-boundary layer, cut-cuticle, l-total leaf, m-mesophyll, s-stomatal		
q			
r_a	aerodynamic resistance above the soil	s m^{-1}	
r_{l, CO_2}	total leaf resistance (stomatal and boundary layer) to CO ₂ diffusion	s m^{-1}	
r_{xd} , concentration-driven	leaf-level water vapor diffusion resistance for concentration driving force, subscripts:	s m^{-1}	
	<i>bd</i> -boundary layer, <i>ld</i> -total leaf, <i>md</i> -mesophyll, <i>sd</i> -stomatal		

$\mathcal{R}$	real numbers		
R	ideal gas constant	J mol ⁻¹ K ⁻¹	
R	rainfall random variable, marked-Poisson process	m	
R_d	rate of dark respiration in absence of photorespiration	mol m ⁻² s ⁻¹	
RH	relative humidity	Pa Pa ⁻¹	
s	relative soil moisture (fraction of saturated soil moisture)	fraction	etc.
s_{vap}	slope of the saturation vapor pressure curve with respect to temperature	Pa K ⁻¹	
S	soil moisture	m	
ΔS	entropy in temperature dependence of photosynthetic parameters		
T	temperature, subscripts: <i>a</i> -air; <i>e</i> -equilibrium, <i>l</i> , <i>leaf</i> -leaf, <i>s</i> -soil, <i>C</i> -Celsius, <i>K</i> -Kelvin	Celsius, Kelvin	
$\mathcal{T}$	finite time horizon		
TPU	rate of phosphate release in triose phosphate utilization	mol m ⁻² s ⁻¹	
u	horizontal wind speed	m s ⁻¹	
$\mathbf{u}$	control process in a stochastic optimal control problem		
$\mathcal{U}$	class of admissible control laws in stochastic differential equation		
V_c	rate of carboxylation of RuBP	mol m ⁻² s ⁻¹	
V_o	rate of oxygenation of RuBP		
$V_{c\max}$	maximum rate of carboxylation		
VPD	vapor pressure deficit	Pa	
w	water vapor mole fraction, suffix: <i>a</i> -ambient air, <i>i</i> -leaf intercellular space, <i>sat</i> -saturated vapor pressure	ppm	
W	water vapor concentration	mol m ⁻³	
$W_{sat}(T)$	saturated water vapor concentration at temperature T	mol m ⁻³	

W_c	rate of carboxylation when RuBP is saturated	mol s ⁻¹ m ⁻²	
W_j	rate of carboxylation when electron transport is limiting	mol s ⁻¹ m ⁻²	
W_p	rate of carboxylation when triose phosphate is limiting	mol s ⁻¹ m ⁻²	
$\mathcal{W}$	Wiener process, subscripts: variable symbol		
X	state variable in stochastic optimal control framework		
Z_r	rooting depth	m	

Symbol	Name	Units	Value
α	exponential mean rainfall depth for random variable H	m	
ϵ	efficiency of light energy conversion for electron transport (empirical expression from Smith, 1937)	mol electrons mol ⁻¹ photons	
ε	rate of change of latent heat content of saturated air with change in sensible heat content	ratio	$\frac{\lambda_{LE}}{c_p} \frac{de_{sat}}{dT}$
γ	psychrometric constant	Pa K ⁻¹	$\frac{P \cdot c_{p,a}}{0.622 \lambda_{H_2O}}$
Γ_*	CO ₂ compensation point	Pa, ppm	
θ	sapwood relative water content	m ³ m ⁻³	
λ	Poisson probability of rainfall for random variable e	d ⁻¹	
λ_{LE}	latent heat of vaporization	J kg ⁻¹	2.454e06 @ 20 °C
λ_R	mean time between rainfalls in Poisson process	d ⁻¹	
ϖ	frequency of periodic process, subscripts: variable symbol	time ⁻¹	
ρ	mass density, subscripts: a -air, l -leaf, H_2O -liquid water	kg m ⁻³	
$\hat{\rho}$	molar density, same subscripts as above	mol m ⁻³	
Φ	legacy function in stochastic optimal control problem		
Φ_{iso}	isothermal radiation	J m ² s ⁻¹	
Φ_{net}	net radiation	W m ⁻²	
Ψ	water potential	MPa	-
Ψ_{soil}	water potential of soil	MPa	
Ψ_{leaf}	water potential of leaf	MPa	
Ψ_M	adiabatic correction for momentum		
Ψ_H	adiabatic correction for heat		
τ			
τ_{Rub}	specificity factor for Rubisco	dimensionless	

Table A.2: Greek symbols

Appendix B

Units and dimensions in leaf gas exchange

Units and dimensions. For gas diffusion, the appropriate driving potential is pressure (or mole fraction = partial pressure / total pressure), rather than concentration, in order to obtain a measure of conductance that is (almost) independent of temperature and pressure (Nobel, 1999, Ch. 8). Temperature and pressure alter the diffusion coefficient of a chemical species as well as the flux density especially for gases, even if the medium's conductive geometry is kept constant. Our desire is to have a measure of the plant's stomatal control that reflects just the stomatal aperture changes, and not temperature and pressure influences on flux density and gas diffusivities. Nobel (1991) derives the stomatal diffusion equation from the general expression for the chemical potential of a gas, which

gives:

$$E(t) = \frac{D_s(t)}{l_i} (W_i(T_{leaf}) - W_a(T_a)) \quad (\text{B.1a})$$

$$= g_{sd} (W_i(T_{leaf}) - W_a(T_a)) \quad (\text{B.1b})$$

where:

$E(t)$ = water vapor flux density [mol H₂O m⁻² s⁻¹]

$D_s(t)$ = diffusion coefficient for water vapor through stomates [m² s⁻¹]

l_i = leaf thickness [m]

W_i, W_a = water vapor concentration inside leaf and in ambient air [mol m⁻³]

T_{leaf}, T_a = temperature of leaf and ambient air [any units]

g_{sd} = stomatal conductance with respect to concentration [m s⁻¹]

The above is a concentration-driven representation of diffusion. However, the diffusion coefficient, D_s , varies with temperature and pressure according to a Clausius-Clapeyron relation, and for gas diffusion this variation is especially pronounced. For plant stomatal conductance, it is preferable to have a measure that does not vary with temperature and pressure in order to examine the plant's stomatal control. Re-working the above equation in terms of pressure as the driving force, rather than concentration, one obtains:

$$E(t) = \frac{D_s(t)}{l_i} (W_i(T_{leaf,K}) - W_a(T_{a,K})) \quad (\text{B.2a})$$

$$= \frac{D_s(t)}{l_i} \left(\frac{P_{v,i}}{R T_{leaf,K}} - \frac{P_{v,a}}{R T_{a,K}} \right) \quad (\text{B.2b})$$

$$\simeq \frac{D_s(t)}{l_i} \left(\frac{P}{R T_{leaf,K}} \right) \left(\frac{P_{v,i}}{P} - \frac{P_{v,a}}{P} \right) \text{ assuming } T_{leaf} = T_a \quad (\text{B.2c})$$

$$E(t) \simeq g_s(t) (w_i(T_{leaf,K}) - w_a(T_{a,K})) \quad (\text{B.3})$$

with:

$$g_s \equiv \frac{D_s(t)}{l_i} \left(\frac{P}{R T_{leaf,K}} \right) \quad (\text{B.4})$$

where:

$P, P_{v,i}, P_{v,a}$ = atmospheric pressure, vapor partial pressures in leaf and air [Pa]
 R = ideal gas constant [$\text{J mol}^{-1} \text{K}^{-1}$]
 $g_s(t)$ = stomatal conductance of water vapor, pressure-driven [$\text{mol m}^{-2} \text{s}^{-1}$]
 $w_i(t)$ = leaf internal water vapor mole fraction [ppm]
 $w_a(t)$ = ambient water vapor mole fraction [ppm]

This gives stomatal conductance, g_s , in terms of $\text{mol-H}_2\text{O m}^{-2} \text{s}^{-1}$, which incorporates correction for temperature and pressure effects on molar flux density, such that g_s does not vary (significantly) due to these ambient effects. This is not a perfect measure, since the difference between the leaf and air temperature can introduce errors (up to 3% for a 10 Kelvin difference, which is a fairly extreme difference; Gu, personal communication), and a Clausius-Clapeyron relation for temperature (T_{leaf}) influences on D_s should be included to be completely rigorous to remove temperature effects (see Nobel, 1991, p. 306, for an exact expression). Given the magnitude of variation observed in diurnal cycles and seasons compared to those small inaccuracies, however, this representation has been deemed satisfactory and most useful for observing and understanding plant stomatal control.

Note that g_s is in molar flux density units, which is appropriate for gases. For heat diffusion, conductance is not on a molar basis, so must be still in m s^{-1} , as for g_{sd} . From now on, the convention here will be to adhere to discussing gas conductances in terms of the molar flux density units, $\text{mol m}^{-2} \text{s}^{-1}$, so that stomatal control by the plant is directly quantified in modeling. Also, since resistances through the leaf stomata to the atmosphere add in series, it will be found more convenient to express the equations in terms of resistances, rather than conductances. This is the approach also preferred by Nobel (1991), Givnish (1986), Lloyd (1991), and Friend (1995). From now on, when speaking

of leaf resistances and conductances, the subscript d will be appended to variables that are in concentration-driven resistance [s m^{-1}] and conductance [m s^{-1}] units, and those corresponding variables *without* the d will be in molar flux density units [$\text{mol m}^{-2} \text{s}^{-1}$] for conductances and the inverse for resistances. Where it is helpful to interconvert stomatal conductance between m s^{-1} and $\text{mol m}^{-2} \text{s}^{-1}$ to compare to other values in the literature, this conversion will be provided.

Appendix C

Farquhar and von Caemmerer (1982) model of photosynthesis

The model of photosynthesis by Farquhar and von Caemmerer (1982) is given below, taken verbatim from Harley, et.al. (1992), who add triose phosphate limitation on the rate carboxylation and give rate constant temperature dependencies. The most rigorous review to date is given in a book by von Caemmerer (2000).

Net assimilation due to the biochemistry of photosynthesis, A_b , is the balance of carboxylation and respiration:

$$A_b = V_c - 0.5V_o - R_d = V_c \left(1 - \frac{0.5 \cdot o}{\tau \cdot c_i} \right) - R_d \quad (\text{C.1})$$

$$A_b = V_c \left(1 - \frac{\Gamma^*}{c_i} \right) - R_d \quad (\text{C.2})$$

where V_c and V_o [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$] are the rate of carboxylation and oxygenation of Rubisco, respectively; c_i and o [ppm] are the mole fractions of CO_2 and O_2 inside the leaf, respectively; R_d [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$] is the rate of dark respiration in absence of

photorespiration. Γ_* [Pa] is the CO₂ compensation point in the absence of mitochondrial respiration, and τ [dimensionless] is a specificity factor for Rubisco. The parameter τ is derived from the Michaelis-Menten competitive kinetics, V_o/V_c , such that (Harley and Tenhunen, 1991):

$$\tau = V_{c\max}K_o / (V_{o\max}K_c) \quad (\text{C.3})$$

where K_c and K_o are Michaelis constants for carboxylation and oxygenation, respectively.

Γ_* and τ are related:

$$\Gamma_* = \frac{0.5 V_{o\max}K_c}{V_{c\max}K_o}o = \frac{0.5 o}{\tau} \quad (\text{C.4})$$

The rate of carboxylation, V_c , is limited by three factors: W_c , carboxylation when ribulose-bisphosphate (RuBP) is saturated, and O₂ and CO₂ compete for RuBP; W_j , carboxylation when the rate of electron transport/photosynthesis limits regeneration of RuBP; and W_p , carboxylation when the rate of triose phosphate transport is limiting, such that:

$$A_b = \min \{W_c, W_j, W_p\} \left(1 - \frac{\Gamma_*}{c_i}\right) - R_d \quad (\text{C.5})$$

These limiting processes are all expressed in terms of Michaelis-Menten dynamics, of the form:

$$W_x = \frac{v_{1,x}c_i}{v_{2,x}c_i + v_{3,x}} \quad (\text{C.6})$$

where the v coefficients which may be constants or temperature-dependent variables.

W_c , carboxylation when ribulose-bisphosphate (RuBP) is saturated, and O₂ and CO₂ compete for RuBP is expressed:

$$W_c = \frac{V_{c\max}c_i}{c_i + K_c(1 + o/K_o)} \quad (\text{C.7})$$

where $V_{c\max}$ is the temperature-dependent maximum rate of carboxylation.

W_j , carboxylation when the rate of electron transport/photosynthesis limits its regeneration of RuBP is expressed:

$$W_j = \frac{J \cdot c_i}{4(c_i + o/\tau)} \quad (\text{C.8})$$

where J is the rate of electron transport, which has been modeled empirically variously.

Harley, et. al. (2001) use an expression by Smith (1937):

$$J = \frac{\epsilon \cdot PAR}{\left(1 + \frac{\epsilon^2 PAR^2}{J_{\max}^2}\right)^{1/2}} \quad (\text{C.9})$$

where ϵ is the efficiency of light energy conversion on an incident light basis (mol electrons / mol photons), $J_{\max}$ is the temperature-dependent light-saturated rate of electron transport.

W_p , carboxylation when the rate of triose phosphate transport is limiting is expressed:

$$W_p = 3 \cdot TPU + \frac{V_o}{2} = 3 \cdot TPU + \frac{V_c \cdot 0.5 \cdot o}{c_i \cdot \tau} \quad (\text{C.10})$$

where TPU is the temperature-dependent rate of phosphate release in triose phosphate utilization.

The temperature dependencies of K_c , K_o , R_d , and τ are described by an Arrhenius relation:

$$\text{Form of } K_c, K_o, R_d, \tau = \exp \left[\mathbf{c} - \frac{\Delta H_a}{R \cdot T_{l,K}} \right] \quad (\text{C.11})$$

where $\mathbf{c}$ is a scaling constant, ΔH_a is an activation energy, R is the gas constant (0.00831 kJ K⁻¹ mol⁻¹), and $T_{l,K}$ is the leaf temperature in Kelvin.

The temperature dependence of $V_{c\max}$, $J_{\max}$, and TPU may be described in the form:

$$\text{Form of } V_{c\max}, J_{\max}, TPU = \frac{\exp[\mathbf{c} - \Delta H_a / (R \cdot T_{l,K})]}{1 + \exp[(\Delta S \cdot T_k - \Delta H_d) / (R \cdot T_{l,K})]} \quad (\text{C.12})$$

where ΔH_d is deactivation energy, and ΔS is an entropy term.

C.1 Parameter values

The parameters R_d , $V_{c\max}$, $J_{\max}$, and TPU are all species-dependent and are determined from leaf gas exchange measurements. R_d is also often roughly estimated as some fraction of $V_{c\max}$ (von Caemmerer, 2000). The light energy conversion efficiency, ϵ , is not a standard parameter to measure, since there are other models for the rate of electron transport, J . For the temperature dependencies of the Rubisco specificity factor, τ , and the Michaelis constants, K_c , K_o , there are only two complete datasets for C3 plants (*Atriplex glabriuscula* by Badger and Collatz, 1977; *Spinaci oleracea* by Jordan and Ogren, 1984). For these biochemical parameters (ϵ , τ , K_c , K_o), the data set by Badger and Collatz (1977) is used extensively in models for other species, including cotton (Harley, et.al., 1992), soybean (Harley, et.al., 1985), a Mediterranean strawberry tree (Harley, et.al., 1986), and broadleaf deciduous trees (Wilson, et.al., 2000), and such parameterization seems to have yielded good model results; however, it should be noted that there is variation in these parameters among species, but how much is not well known. For ϵ and the temperature dependent parameterizations of τ , K_c , and K_o (Equation C.11 the values of Harley, et.al. (1992) are used here, given in Table C.1.

Parameter	Units	Value
ϵ	mol CO ₂ / mol photon	0.06
$\mathbf{c}(K_c)$	kJ mol ⁻¹	31.95
$\Delta H_a(K_c)$	kJ mol ⁻¹	65.0
$\mathbf{c}(K_o)$	kJ mol ⁻¹	19.61
$\Delta H_a(K_o)$	kJ mol ⁻¹	36.0
$\mathbf{c}(\tau)$	kJ mol ⁻¹	-3.949
ΔH_a	kJ mol ⁻¹	-28.99

Table C.1: Temperature dependencies of biochemical parameters

C.2 Relation of $\mathbf{A}_b$ to $\mathbf{g}_s$

The above gives the biochemical equation for assimilation, A_b , i.e. what is happening inside the leaf, as driven by the leaf internal CO₂ concentration, C_i . The concentration C_i is also constrained by the rate of supply through the stomates, and hence by stomatal conductance and the physics of diffusion (Equation 4.12). The full leaf C_i budget equation therefore shows the explicit relationship between assimilation and stomatal conductance.

Appendix D

Leaf boundary layer conductances/resistances

Leaf boundary layer resistances are calculated following flat plate theory in fluid mechanics. Leaf boundary layer modeling is reviewed by Schuepp (1993), with critical values for leaves investigated by Grace (1981). Textbook overviews may be found in Monteith and Unsworth (1990), Campbell (1986), and Jones (1992), and definitions of non-dimensional quantities for heat and mass transfer are summarized in Kreith and Bohn (2001) and Incropera and DeWit (2002). Here, a concise summary suitable for application is provided.

Fluid flow fields within a boundary layer are either *laminar* (streamlines parallel) or *turbulent* (streamlines chaotic), and the transition from laminar to turbulent flow may be predicted by thresholds of the Reynolds number ($Re = u * d / \nu_k$, u = free-stream fluid velocity, d =flat plate length, ν_k =kinematic viscosity). The velocity profile of the boundary

layer in laminar flow is parabolic, with the no-slip condition at the surface, increasing to the free-stream velocity. The velocity profile in turbulent flow has a thin viscous laminar sublayer with a roughly linear profile dominated by diffusion, then a buffer layer in which diffusion and turbulent mixing are comparable, and then the turbulent zone in which the profile is constant. In addition to the parameters in Re , the transition from laminar to turbulent flow is influenced by surface roughness and ambient turbulence in the free stream.

The means of heat and mass transfer through the boundary layer is via diffusion-type relations across the boundary layer, with the diffusion coefficient influenced by the type of flow field and by the balance between different transport forces as summarized by the Navier-Stokes equations (diffusivity, momentum, viscosity, buoyancy). The balance among these determines the relative importance of transfer by *forced convection* (fluid motion) or *free convection* (change in fluid density due to temperature gradients, also called *natural convection*). Both kinds of convection are possible in both laminar and turbulent flow.

In laminar flow, the velocity profile with forced convection is the usual laminar flow parabolic profile. In the case of free convection, for a surface that is not perfectly horizontal, the temperature-induced change in buoyancy leads to an enhanced velocity profile within the boundary layer, which then declines back to the free stream velocity (the buoyancy speeds up flow in the boundary layer). Instabilities caused by free convection can lead to transition from laminar to turbulent flow sooner than Re would predict, and this transition is correlated with the Rayleigh number, which is the product of the Grashof and Prandtl number, $Ra = Gr * Pr$, $Ra_{crit} = 10^9$. In practice, free convection is hardly ever significant in turbulent flow. In general, when it is unclear whether forced or free convection dominate,

Phenomenon	Heat transfer	Mass transfer	Critical Value
conductance [m s ⁻¹]	$g_H = D_H^* \text{Nu}/d$	$g_X = D_X^* \text{Sh}/d$	–
momentum/viscous forces and laminar-turbulent transition	$\text{Re} = u^* d / \nu_k$	same	See list below
buoyancy-induced transition to turbulence, thermal	$\text{Ra} = \text{Gr}^* \text{Pr}$	same	10^9
free/forced convection	Gr/Re^2	same	1
dimensionless gradient	$\text{Nu} = f(\text{Re}, \text{Ra}, \text{Pr})$	$\text{Sh} = f(\text{Re}, \text{Gr}, \text{Sc})$	–
ratio of momentum to diffusivities	$\text{Pr} = \nu_k / D_H$	$\text{Sc} = \nu_k / D_X$	
ν_k [m ² s ⁻¹] = kinematic viscosity, D_H [m ² s ⁻¹] = thermal diffusivity, D_X [m ² s ⁻¹] = diffusivity of species X			

Table D.1: Non-dimensional relations for boundary-layer heat and mass transfer.

the transfer coefficients for both are calculated separately, and the larger one is used.

In general, relations for forced convection for a flat plate are well-known. Relations for free convection still are subjects of research, with differences due to whether the plate is inclined, vertical, or horizontal, and whether the upper vs. lower surface is hot. There is similarity between heat transfer and mass transfer, such that their relevant non-dimensional parameters obey parallel empirical relations, as shown in the table below.

The length scale for a leaf should approximate its equivalent flat plate, which is given approximately by the average length of the leaf (see more precise formula in Campbell), or by the area/perimeter ratio.

Given the above non-dimensional relations, calculation of conductance g_H (thermal) or g_X (mass) can follow the steps below:

1. Flow field: Check Re and Ra for laminar vs. turbulent flow.

Type of flow	Internal flow	External flow
laminar	$0 < \text{Re} < 2100$	$0 < \text{Re} < 500,000$
transitional	$2100 < \text{Re} < 4000$	$200,000 < \text{Re} < 3,000,000$
turbulent	$4000 < \text{Re}$	$1,000,000 < \text{Re}$

Table D.2: Reynolds number critical values.

2. Type of convection: Check Gr/Re^2 for free vs. forced convection.
3. Given 1 and 2, calculate Nu for heat transfer, Sh for mass transfer.
4. Calculate the conductance as function of diffusivity, Nu or Sh , and length scale.

Reynolds number, $\text{Re} = \mathbf{u} \cdot \mathbf{d}/\nu_k$

For the Reynolds number, Re , critical values from flat plate theory are (F.M. White, 1979; Munson, Young, and Okiishi, 1998):

In practice, the critical value for transition to turbulent flow is $\text{Re}_{crit} = 500,000$. For leaves, Re_{crit} may be smaller due to surface irregularities, and Grace (1981) gives a range of $\text{Re}_{crit} = 400\text{-}3000$.

Sherwood number

The Sherwood number gives the relation between advective versus diffusive mass transport. It is calculated here as follows, checking for different flow conditions:

Under laminar flow ($\text{Re} < \text{Re}_{crit}$ and $\text{Ra} < 10^9$) and free convection ($\text{Gr}/\text{Re}^2 > 1$), $\text{Sh} = 0.54 * (\text{Gr} * \text{Sc})^{0.25}$ (Campbell, 1977).

Under laminar flow and forced convection, $\text{Sh} = 0.664 \cdot \text{Re}^{1/2} \cdot \text{Sc}^{1/3}$ (Kreith and Bohn, 2001).

Under turbulent flow ($\text{Re} \geq \text{Re}_{crit}$ or $\text{Ra} \geq 10^9$), $\text{Sh} = 0.036 * \text{Sc}^{1/3} * \text{Re}^{0.8}$ (Kreith

and Bohn, 2001).

where:

Grashof number, $Gr = \frac{d^3 \cdot g \cdot \beta (T_{surface} - T_{fluid})}{\nu_k}$, gives the proportion between buoyancy force and viscous force

Prandtl number, $Pr = \frac{\nu_k}{D_H}$, gives the proportion between momentum diffusivity (kinematic viscosity) and thermal diffusivity

Schmidt number, $Sc = \frac{\nu_k}{D_X}$, gives the proportion between kinematic viscosity and molecular diffusivity

Nusselt number, Nu , gives the proportion between total heat transfer and conductive heat transfer (details in Kreith and Bohn, 2001)

Rayleigh number, $Ra = Gr \cdot Pr$.

The boundary-layer resistance for a leaf is then (Schuepp, 1993):

$$r_b = \frac{D_{H_2O}(T_a) \cdot Sh(u, l_{leaf}, \nu_{k,a}, D_{H_2O}, T_{l,surf}, T_a)}{l_{leaf}} \quad (D.1)$$

Appendix E

Heat pulse velocity (HPV) estimation of sap flow

The calculation procedure used for calculating sap flow from heat pulse velocity (HPV) is given below. Note that by "sap flow" is meant the volume flow rate of sap through an individual tree. The steps in order are:

1. Calculation of heat pulse velocity from temperature time traces.
2. Correction for sensor misalignment.
3. Correction for wounding.
4. Calculation of sap velocity from heat pulse velocities.
5. Calculation of individual tree sap flow from tree bole radial profiles of sap velocity.

E.1 Calculation of heat pulse velocity

Calculation of sap velocity followed the heat ratio method refined by Burgess, et.al. (2001). Initial temperatures are measured, averaged for 10 seconds at 0.5 Hz, and then the heater probe is turned on for 2 seconds. A minute and 15 seconds are allowed to pass

for the transport of heat to reach an equilibrium and then the last 40 seconds of 0.5 Hz temperature traces are used to calculate heat pulse velocities using the heat ratio method. The following equation is the basic calculation of heat pulse velocity, *HPV*, if all probes are installed perfectly in the tree:

$$HPV = \frac{\alpha}{x} \cdot \underset{40 \text{ sec}}{mean} \left(\ln \frac{\Delta T_{upper,t}}{\Delta T_{lower,t}} \right) \cdot (\text{seconds per hour}) \quad (\text{E.1})$$

where:

HPV [cm hr⁻¹] = heat pulse velocity
 α [cm² s⁻¹] = thermal diffusivity of the sapwood
 x [cm] = distance between the heater probe and the thermocouple probes
 $\Delta T_{upper,t}$, $\Delta T_{lower,t}$ [°C] = temperature change from initial temperature at time t

Since probes may be misaligned, however, corrections must be made by accounting for asymmetrical positions of the thermocouple probes.

E.2 Correction for sensor misalignment

Correction for sensor misalignment can be done by calibrating the heat pulse data against times when sap flow is known to be zero or close to zero. This involves solving the following equation of adjusted heat pulse velocity, V_h , for asymmetrical distances between each thermocouple probe and the heater probe:

$$V_h = \frac{(4\alpha t \cdot \ln \left(\frac{\Delta T_{upper,t}}{\Delta T_{lower,t}} \right) - (x_{lower}^2 - x_{upper}^2))}{2t(x_{upper} - x_{lower})} \cdot (\text{seconds per hour}) = 0 \quad (\text{E.2})$$

where:

V_h [cm hr⁻¹] = corrected heat pulse velocity
 x_{lower} , x_{upper} [cm] = distances of upstream and downstream thermocouple probes from the heater probe
 t [s] = time since end of heat pulse

Since there are two unknowns, x_{lower} and x_{upper} , for one equation, the equation is solved twice, assuming one of the two distances is correct. Since it is not known which solution is correct, the corrected heat pulse velocity for all times, including non-zero sap flow, is taken to be the mean $\bar{V}_h$ from calculating V_h using both values.

E.3 Correction for wounding

Because of wounding effects which reduce the flow of sap around the probes, further correction to the heat pulse velocity calculations must be made for the effective loss of conductivity in the vicinity of the probes. Burgess, et.al. (2001) obtained correction coefficients for a range of wound diameters to be applied in the follow equation to calculate wound-corrected heat pulse velocity, V_c :

$$V_c = B_{wound} \cdot \bar{V}_h \tag{E.3}$$

where B_{wound} is linearly related to the wound diameter, according to Burgess, et.al.'s (2001) tests. Since Burgess, et.al.'s (2001) correction factors were for averages of measurements taken 60-100 s after the release the heat pulse, whereas the data for Ione were from 70-110 s to ensure strong linearity in the heat ratios with time, Burgess, et.al.'s (2001) numerical model was re-calculated for the later time series. The new correction coefficients are given in Table E.1.

For oak trees, the wound space was estimated to be at least an annulus as wide as a large blue oak vessel if one were broken by the probes, the largest being 0.4 mm. Therefore, the needle sensor diameter of 1.275 mm plus double the annulus width gives an oak wound diameter of 2.075 mm.

wound diameter (mm)	B wound correction coefficient
1.7	1.6569
1.8	1.7096
1.9	1.7727
2.0	1.8314
2.1	1.8924
2.2	1.9558

Table E.1: Wound correction factors for correcting heat pulse velocities to sap velocities, for use with averages of data measured 70-110 s following the release of the heat pulse. Obtained from recalculations of the B factor in the numerical model of Burgess, et.al. (2000).

For the grey pines, the wound diameter used was that found by Meredith Bauer for *Pinus ponderosa* (personal communication) through dye techniques on cut trees, 1.8 mm. Checking this value against the estimation method for the oaks, given a pine pore diameter of about 0.26, the estimated wound diameter would be 1.795, close to the measured value for pine. Therefore, the estimate for blue oaks is considered satisfactorily close to the actual values.

E.4 Calculation of sap velocity from heat pulse velocity

Conversion of the heat pulse velocity values to sap velocity, V_s , finally involves scaling against the wood thermal properties with the following equation:

$$V_s = V_c \rho_{wood} \cdot \frac{(c_{p,wood} + \Phi_{sat} \cdot c_{p,sap})}{\rho_{sap} \cdot c_{p,sap}} \quad (E.4)$$

where:

- V_s [cm hr⁻¹] = sap velocity
- ρ_{wood} [kg m⁻³] = density of wet woody cell wall
- ρ_{sap} [kg m⁻³] = density of sap, same as water
- $c_{p,wood}$ [J kg⁻¹K⁻¹] = dry wood specific heat
- $c_{p,sap}$ [J kg⁻¹ K⁻¹] = sap specific heat, same as water
- Φ_{sat} [vol vol⁻¹] = saturated wood moisture content

Note that this equation can be modified to account for changing wood moisture content.

E.5 Integration of sap velocities to tree sap flow

Having the radial profile of sap velocities, the calculation of the whole tree sap flow rate, F_{tree} , simply involves integrating the radial profile over the sapwood area, and correcting for the presence of ray cells:

$$F_{tree} = (1 - \Upsilon) \int_{r_{in}}^{r_{out}} V_s r dr d\theta \quad (E.5)$$

where:

- F_{tree} [cm³ hr⁻¹] = tree sap flow (volume per time)
- Υ [fraction] = fraction of sapwood area covered by ray cells
- r [cm] = radial distance from the center of the tree bole
- r_{in} [cm] = inner radial limit, sapwood-heartwood boundary
= tree radius - sapwood thickness
- r_{out} [cm] = outer radial limit of sapwood
= tree radius
- θ [radians] = angle around the tree bole

Since the data were in discrete samples of V_s at just 2-3 radial points in the sapwood, linear interpolation was performed between measurements, and it was assumed that the sap velocity is zero at r_{out} , the sapwood-heartwood boundary. When the outer edge sapwood velocity data were poor (due to environmental noise), the trend of the inner probe values was extrapolated outward, or the outer value was set equal to the value of the adjacent radial measurement if extrapolation was negative in slope (it was assumed that the outer xylem still must have greater conductivity on average).

Finally, since ray cells form a significant part of the sapwood, the overall sap flow was corrected by their sapwood areal fraction.

The sap flux density, f_{sap} [$\text{cm}^3 \text{ hr}^{-1} / \text{cm}^2 = \text{cm hr}^{-1}$], can further be calculated from the sap flow rate, F_{tree} , simply by dividing by the sapwood area of the tree. The sap flux density then is the useful quantity for performing scaling of tree sap flow to stand-level transpiration.

Appendix F

Sap flow circuitry

The following diagram of sap flow probe circuitry shows the wiring for one (1) sap flow probe, which consists of two copper-constantan thermocouple probes and one heater coil, each enclosed in glass pipettes inside a 1.275 mm diameter surgical needle. The diagram shows the connections of the thermocouple junctions to a Campbell Scientific AM416 multiplexer, which is connected to a Campbell CR10X datalogger. The heater coil is connected to a relay switch that switches it on and off, as signaled from the CR10X. For the measurements at the Ione savanna site, the sap flow probe connections were iterated 5 times over a multiplexer for each datalogger/multiplexer set-up.

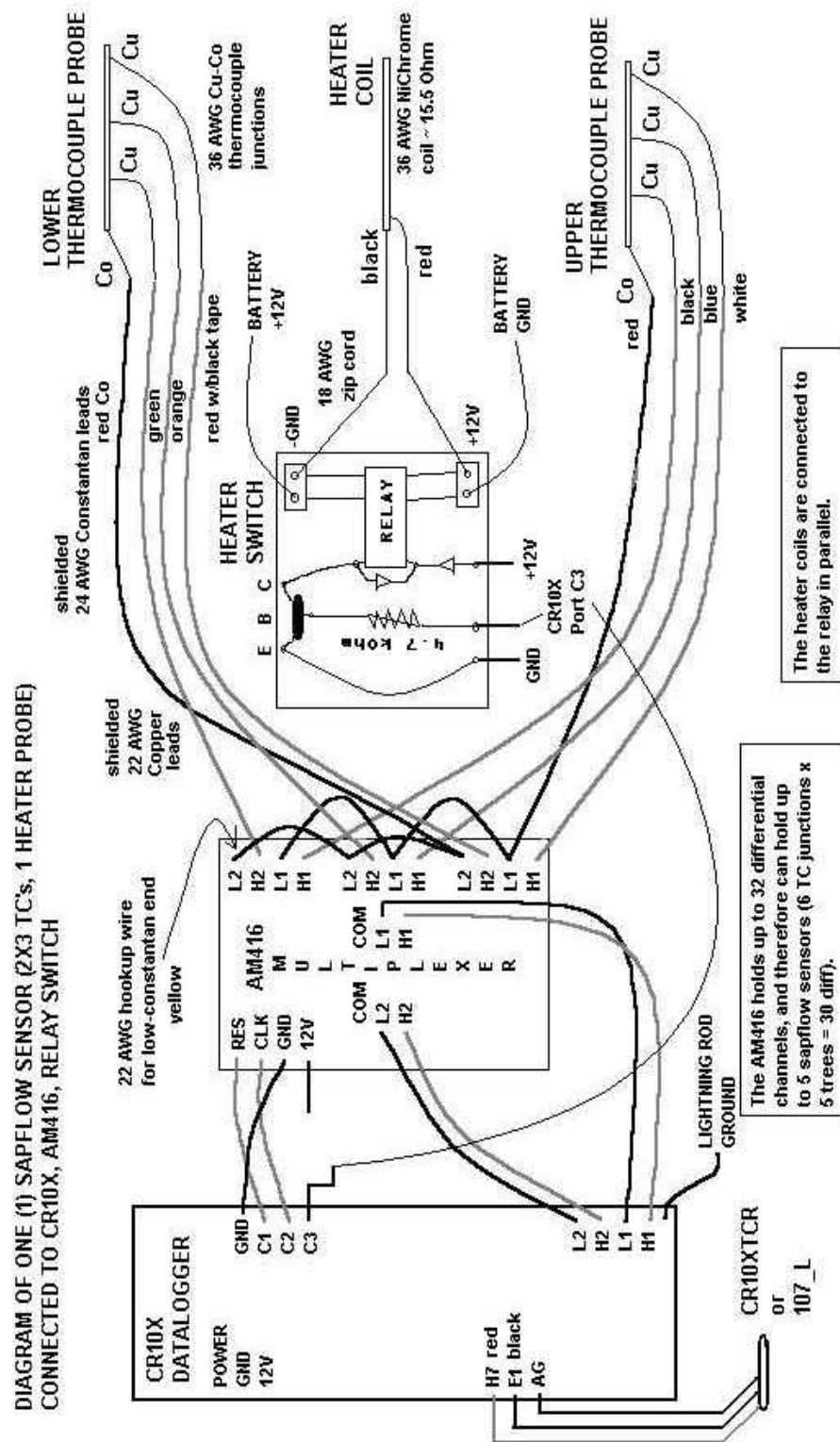


Figure F.1: Diagram of circuitry for one (1) heat-pulse velocity (HPV) sap flow sensor.

Appendix G

Alternating Conditional Expectations Algorithm (Breiman and Friedman, 1985)

The Alternating Conditional Expectations (ACE) algorithm is given by Breiman and Friedman (1985), "Estimating optimal transformations for multiple regression and correlations (with discussion)," *Journal of the American Statistical Association*, 80: 580-619. ACE is a non-parametric algorithm that iteratively maximizes correlation in least-squares fashion between the predictor and response variables, producing transformed relations that identify non-linearities that are not known *a priori*. These transformations fit into the scheme of generalized additive models (GAM), which have the general form:

$$t(Y) = \sum_i f_i(X_i) \tag{G.1}$$

where Y is the response variable, X_i are the predictor or explanatory variables, and t and f_i are their respective, possibly non-linear, transformations that maximize correlation within the GAM framework.

The algorithm is as follows for the case of a single predictor variable: Given a predictor, X , and a response, Y , the strategy of ACE is to find the minimum of the expected value of the difference between $t(Y)$ and $f(X)$:

$$\text{Objective: } \min E \{t(Y) - f(X)\}^2 \quad (\text{G.2})$$

$$\text{given: } f(X) = E \{t(Y) | X\} \quad (\text{G.3})$$

$$\text{and: } t(Y) = E \{f(X) | Y\} \quad (\text{G.4})$$

1. Initialize $t(Y)$:

$$t(Y) = \{Y - E \{Y\}\} / \sqrt{\text{var}(Y)} \quad (\text{G.5})$$

2. Calculate $f(X)$. This can be done using a non-parametric, local smoother, such as that of Friedman and Stuetzle (1982):

$$f(X) = E \{t(Y) | X\} \quad (\text{G.6})$$

- 3a. Compute an estimate $\tilde{t}(Y)$:

$$\tilde{t}(Y) = E \{f(X) | Y\} \quad (\text{G.7})$$

- 3b. To get a unique solution, standardize the result in 3a to get a new $t(Y)$:

$$t(Y) = \frac{\tilde{t}(Y) - \bar{Y}}{\sqrt{\text{var}(\tilde{t}(Y))}} \quad (\text{G.8})$$

4. Alternate between steps 2 and 3 until $E \{t(Y) - f(X)\}^2$ meets some minimum value criterion.

For the multivariate case with p predictor variables, one just expands the single variable case, replacing steps 2-4 as:

2. Calculate $f_1, \dots, f_p$:

$$\langle f_1(X_1), \dots, f_p(X_p) \rangle = E \{t(Y) | X_1, \dots, X_p\} \quad (\text{G.9})$$

3a. Compute an estimate $\tilde{t}(Y)$:

$$\tilde{t}(Y) = E \{(\sum f_i X_i) | Y\} \quad (\text{G.10})$$

3b. Standardize to get $t(Y)$.

4. Iterate 2-3 until convergence is obtained in $E \{t(Y) - f(X)\}^2$.

Appendix H

Statistical distributions of storm arrival times and storm depths for Ione, California, climate

Weather data from the California Department of Water Resources Station Ben Bolt were used to parameterize the rainfall model of Rodriguez-Iturbe, et.al. (2001). Below are histograms by season (wet winter, spring, summer dry) of storm arrival time and storm depth, which were fitted to a marked-Poisson model of rainfall.

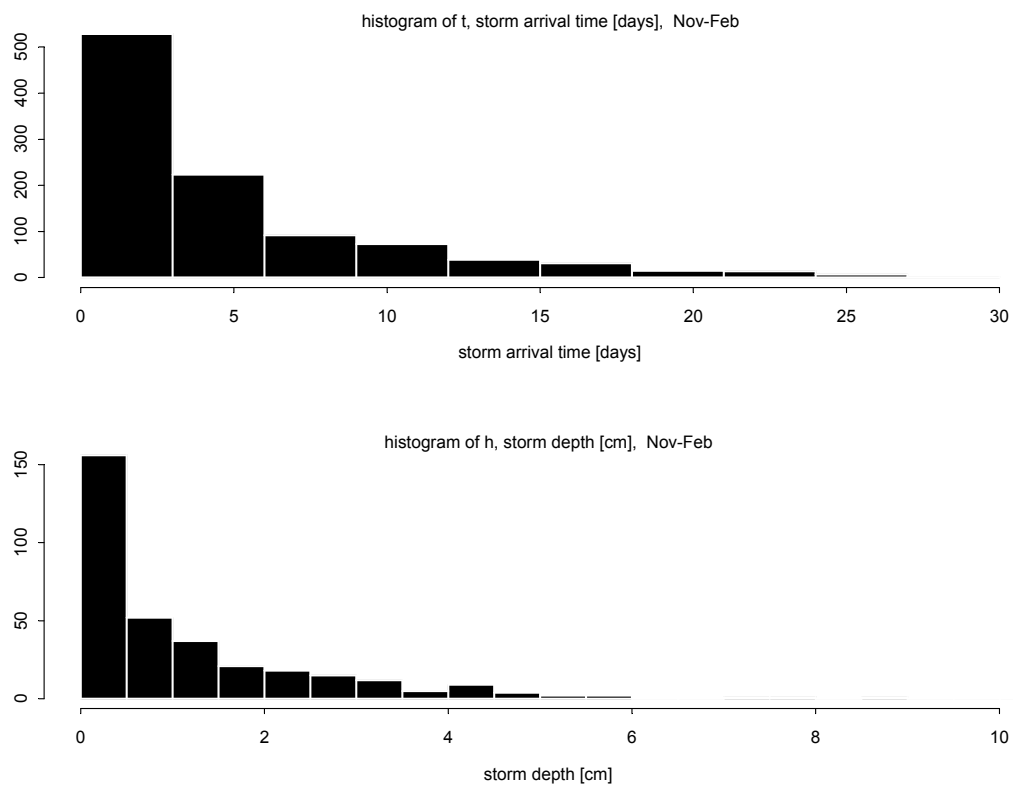


Figure H.1: Histograms for winter storm arrival time, t , and storm depth, h (CDWR Station Ben Bolt, 1988-1999).

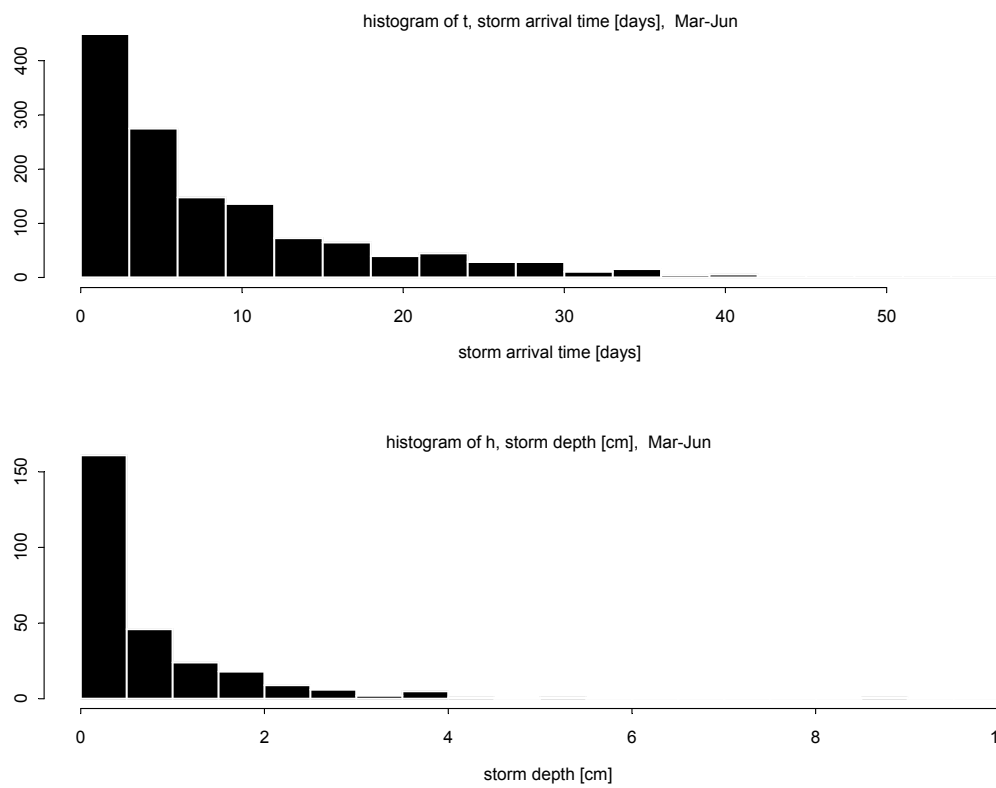


Figure H.2: Histograms for spring storm arrival time, t , and storm depth, h (CDWR Station Ben Bolt, 1988-1999).

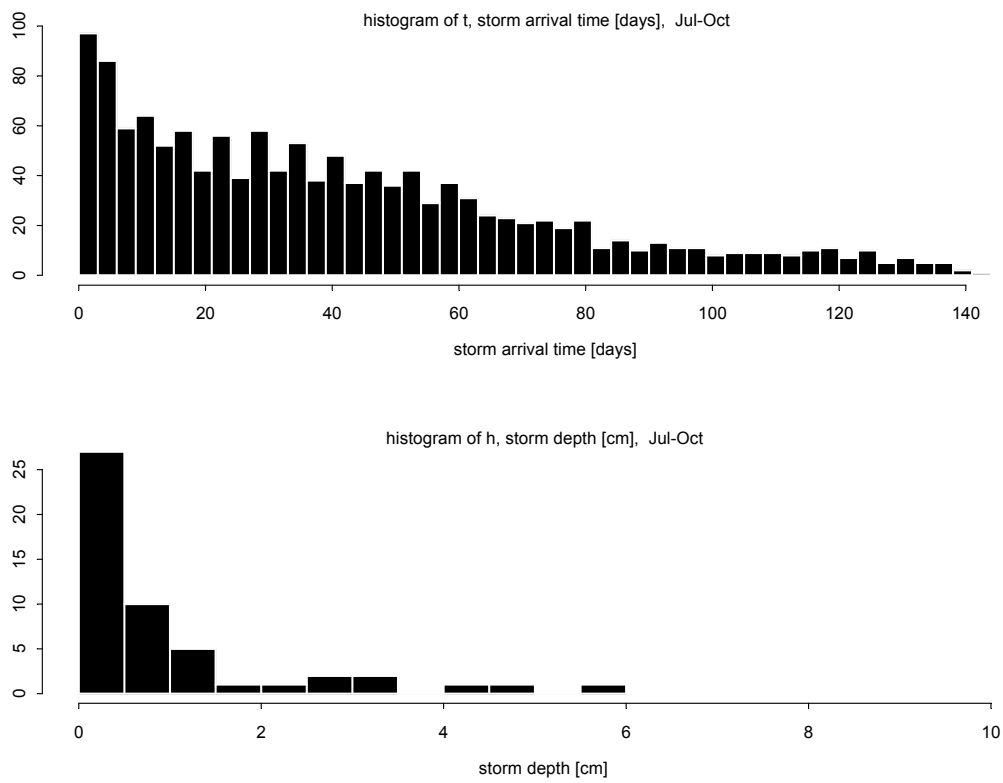


Figure H.3: Histograms for summer storm arrival time, t , and storm depth, h (CDWR Station Ben Bolt, 1988-1999).

Appendix I

Probabilistic soil moisture functions of Rodriguez-Iturbe and co-workers (2001)

The following functions for the probability density functions of soil moisture and dynamic water stress are derived in the set of papers by Rodriguez-Iturbe, et.al. (2001, Laio, et.al., (2001a, and Porporato, et.al. (2001. All terms are provided in the Table I.1.

Soil moisture, s , is the normalized soil moisture or relative soil moisture content equal to 1 at saturation and 0 at the hygroscopic or minimum soil moisture content. Likewise, fluxes from the soil are normalized by the soil moisture holding capacity (porosity, n , times depth of active soil or rooting depth, Z_r), so that normalized minimum and maximum

Symbol	Definition
E	evapotranspiration rate, cm d^{-1} ; subscripts: max-average daily rate under unrestricted soil moisture, w-average daily rate at $s=s_w$
L	leakage or deep infiltration rate, cm d^{-1}
k	dynamic stress parameter to account for plant resistance to stress
K_s	saturated hydraulic conductivity, cm d^{-1}
m	symbol for expression in the function of leakage loss rate, d^{-1}
n	soil porosity, dimensionless
q	parameter defining the non-linearity of the static water stress, dimensionless
s	relative soil moisture, dimensionless; subscripts: fc-field capacity, h-hygroscopic or minimum soil moisture point, w-wilting point
t	time, days; subscripts for soil-drying process: s_{fc} -time to reach $s=s_{fc}$, s_w -time to reach $s=s_w$, s^* -time to reach $s=s^*$
Z_r	depth of active soil or root depth, cm
T_{seas}	duration of growing season, days
T_{s^*}	average duration of an excursion of the trajectory of soil moisture below s^* , days
β	parameter in exponential expression for the relation between hydraulic conductivity and soil moisture, dimensionless
ζ	static water stress, dimensionless
$\bar{\zeta}$	average static water stress, dimensionless
η	normalized average daily evapotranspiration rate, d^{-1} ; subscripts: none-unrestricted soil moisture conditions, w-rate at $s=s_w$
λ'	arrival rate of rainfall events that reach the ground (accounting for interception)
ρ_{loss}	normalized soil water loss rate, d^{-1}

Table I.1: Table of symbols for expressions of probabilistic soil moisture (Rodriguez-Iturbe, et.al., 2001).

evapotranspiration (soil evaporation and vegetation transpiration combined) are:

$$\eta_w = \frac{E_w}{nZ_r}, \text{ wilting point} \quad (\text{I.1})$$

$$\eta = \frac{E_{\max}}{nZ_r}, \text{ unstressed} \quad (\text{I.2})$$

The soil's rate of moisture loss, the loss function, ρ_{loss} , is expressed as a function of soil moisture, with losses due to evapotranspiration and leakage:

$$\rho_{loss} = \frac{E(s) + L(s)}{nZ_r} \quad (\text{I.3})$$

$$= \left\{ \begin{array}{ll} 0 & 0 < s \leq s_h \\ \eta_w \frac{s-s_h}{s_w-s_h} & s_h < s \leq s_w \\ \eta_w + (\eta - \eta_w) \frac{s-s_w}{s_*-s_w} & s_w < s \leq s_* \\ \eta & s_* < s \leq s_{fc} \\ \eta + m \left(e^{\beta(s-s_{fc})} - 1 \right) & s_{fc} < s \leq 1 \end{array} \right\} \quad (\text{I.4})$$

The decay in soil moisture over time during a period of no rainfall is given by:

$$s(t) = \left\{ \begin{array}{ll} s_0 - \frac{1}{\beta} \ln \left[\frac{\eta - m + m e^{\beta(s_0-s_{fc})} e^{\beta(\eta-m)t} - m e^{\beta(s_0-s_{fc})}}{\eta - m} \right] & 0 \leq t < t_{s_{fc}} \\ s_{fc} - \eta (t - t_{s_{fc}}) & t_{s_{fc}} \leq t < t_{s_*} \\ s_w + (s_* - s_w) \times & t_{s_*} \leq t < t_{s_w} \\ \left[\frac{\eta}{\eta - \eta_w} \exp \left(-\frac{\eta - \eta_w}{s_* - s_w} (t - t_{s_*}) \right) - \frac{\eta_w}{\eta - \eta_w} \right] & \\ s_h + (s_w - s_h) \exp \left(-\frac{\eta - \eta_w}{s_w - s_h} (t - t_{s_w}) \right) & t_{s_w} \leq t < \infty \end{array} \right\} \quad (\text{I.5})$$

where

$$m = \frac{K_s}{nZ_r \left(e^{\beta(1-s_{fc})} - 1 \right)} \quad (\text{I.6})$$

$$t_{s_{fc}} = \frac{1}{\beta(m-\eta)} \left[\beta(s_{fc} - s_0) + \ln \left(\frac{\eta - m + me^{\beta(s_0 - s_{fc})}}{\eta} \right) \right] \quad (\text{I.7})$$

$$t_{s^*} = \frac{s_{fc} - s^*}{\eta} + t_{sf} \quad (\text{I.8})$$

$$t_{s_w} = \frac{s^* - s_w}{\eta - \eta_w} \ln \left(\frac{\eta}{\eta_w} \right) + t_{s^*} \quad (\text{I.9})$$

The probability density function of soil moisture, $p(s)$, is given by:

$$p(s) = \left\{ \begin{array}{ll} 0 & 0 < s \leq s_h \\ \frac{C}{\eta_w} \left(\frac{s-s_h}{s_w-s_h} \right)^{\frac{\lambda'(s_w-s_h)}{\eta_w}-1} e^{-\gamma s} & s_h < s \leq s_w \\ \frac{C}{\eta_w} \left[1 + \left(\frac{\eta}{\eta_w} - 1 \right) \left(\frac{s-s_w}{s^*-s_w} \right) \right]^{\frac{\lambda'(s^*-s_w)}{\eta-\eta_w}-1} e^{-\gamma s} & s_w < s \leq s_* \\ \frac{C}{\eta} e^{-\gamma s + \frac{\lambda'}{\eta}(s-s^*)} \left(\frac{\eta}{\eta_{s_w}} \right)^{\lambda' \frac{s^*-s_w}{\eta-\eta_w}} & s_* < s \leq s_{fc} \\ \frac{C}{\eta} e^{-\gamma s + \frac{\lambda'(s-s^*)}{\eta}-1} \left(\frac{\eta e^{\beta s}}{(\eta-m)e^{\beta s_{fc}} + me^{\beta s}} \right)^{\frac{\lambda'}{\beta(\eta-m)}+1} & s_{fc} < s \leq 1 \\ \times \left(\frac{\eta}{\eta_w} \right)^{\lambda' \frac{s^*-s_w}{\eta-\eta_w}} e^{\frac{\lambda'}{\eta}(s_{fc}-s^*)} & \end{array} \right\} \quad (\text{I.10})$$

where C is a constant whose expression may be obtained analytically, as provided in an appendix in Laio, et.al., 2001a. However, due to the piecewise form of the expression and the presence of the bound, the practice by one of the co-workers (Amilcare Porporato, personal communication) was followed, directly calculating C from integrating over $p(s)$ and normalizing using this result.

Water stress experienced by vegetation at a given time, $\zeta(t)$, "static water stress," is expressed by Porporato, et.al. (2001) simply as a scaling between the soil moisture critical points s^* and s_w :

$$\zeta(t) = \frac{[s^* - s(t)]^q}{s^* - s_w}, \text{ for } s_w \leq s(t) \leq s^* \quad (\text{I.11})$$

where q is a "measure of the nonlinearity of the effects of soil moisture deficit on plant conditions." Porporato, et.al, (2001) remark that the value of q can vary with plant species,

as do s^* and s_w . This is one parameter that is not easily quantified and that has little physiological basis, though conceptually it lends thoroughness to this hydrologists' model by taking into account the variation in plant drought responses. Since q is not easily known, a default linear relation, $q = 1$, is used here. Porporato, et.al., (2001) and Laio, et.al. (2001b), perform investigations of how much differences in q can affect the quantification of water stress.

The "dynamic water stress," $\bar{\theta}$, quantifies the total stress experienced by vegetation over a period of time. For a growing season, it was calculated according to Equation 28 in Porporato, et.al., (2001), but modified so that the stress level is not conditional on the existence of stress but includes periods of no water stress also to cover whole seasons:

$$\bar{\theta} = \left\{ \begin{array}{ll} \left(\frac{\overline{\zeta T_{s^*}}}{kT_{seas}} \right)^{1/\sqrt{\overline{n_{s^*}}}} & \text{if } \overline{\zeta T_{s^*}} < kT_{seas} \\ 1 & \text{otherwise} \end{array} \right\} \quad (\text{I.12})$$

Appendix J

Hamilton-Jacobi-Bellman equation

J.1 Control problem

A **control problem** is defined as the problem to maximize the expected value of the time integral of the value function:

$$\mathcal{J}(t, x, \mathbf{u}) = E_{t,x} \left\{ \int_t^T F(s, X_s^{\mathbf{u}}, \mathbf{u}_s) ds + \Phi(X_T^{\mathbf{u}}) \right\} \quad (\text{J.1})$$

given that one started at state x at time t , and certain dynamics of state variable $\mathbf{X}$ and constraints on control process $\mathbf{u}$. Here, lower-case $t \in R_+$ and $x \in R^n$ denote fixed points, and $\mathbf{u} \in R^k$ in our case is adapted to the state process $\mathbf{X}$, such that $\mathbf{u}_t = \mathbf{u}(t, X_t)$. Φ is a "legacy" function, which measures the utility of having some resources left over at the end of the period $[t, T]$.

The time dynamics of $\mathbf{X}$ are expressed in a **controlled** stochastic differential equation (SDE):

$$dX_t = \mu(t, X_t, \mathbf{u}(t, X_t)) dt + \sigma(t, X_t, \mathbf{u}(t, X_t)) dW_t + \xi(t, X_t, \mathbf{u}(t, X_t)) dY_t \quad (\text{J.2})$$

$$X_t = x \tag{J.3}$$

where $\mu(t, X_t, \mathbf{u}(t, X_t)) \in R^n$ is a deterministic influence, $W \in R^n$ is a Wiener process whose variance is scaled by the matrix $\sigma(t, X_t, \mathbf{u}(t, X_t)) \in R^{n \times d}$ at time t , and $Y \in R^l$ is a Poisson process marked by a magnitude $\xi(t) \in R^{n \times l}$ that may also be a random variable.

The Wiener process W represents random drift in X , and is a stochastic process with the following properties (as defined in Björk, 1998):

1. $W(0) = 0$.
2. The process W has independent increments, i.e. if $r < s \leq t < u$ then $W(u) - W(t)$ and $W(s) - W(r)$ are independent stochastic variables.
3. For $s < t$ the stochastic variable $dW = W(t) - W(s)$ has the Gaussian distribution $N(0, \sqrt{t-s})$, i.e. if $dt = t-s$, then $dW \sim N(0, \sqrt{dt})$.
4. W has continuous trajectories.

The marked-Poisson process ξY describes the occurrence of random events of random magnitude, and is a stochastic process with the following properties:

1. Y is a Poisson process with mean rate of occurrence $E(Y)$, such that: the stochastic variable $dY = Y(t) - Y(s)$

$$= \left\{ \begin{array}{l} 1 \text{ with probability } E(Y) dt \\ 0 \text{ with probability } 1 - E(Y) dt \end{array} \right\}, s < t$$
2. All such dY are independent.
3. ξ is an exponential random variable with mean $E(\xi)$, such that:

$$f_\xi(\xi_t) = \frac{1}{E(\xi)} \exp\left(-\frac{\xi_t}{E(\xi)}\right)$$
 where ξ_t is an instance of ξ .

The problem has the constraints:

$$\mathbf{u}(s, y) \in \mathcal{U}, \forall (s, y) \in [t, T \times R^n] \tag{J.4}$$

where $\mathcal{U}$ is the class of admissible controls laws, which requires that for any given initial point (t, x) , the above SDE has a unique solution. (Note that s, y are used for the variables, since t and x denote the fixed points).

J.2 Hamilton-Jacobi-Bellman equation derivation

Let us denote $\widehat{\mathcal{J}}$ as the optimal value function:

$$\widehat{\mathcal{J}}(t, x) = \widehat{\mathcal{J}}(t, X_t^{\widehat{\mathbf{u}}}, \widehat{\mathbf{u}}) = \sup_{\mathbf{u} \in \mathcal{U}} \mathcal{J}(t, x, \mathbf{u}) \quad (\text{J.5})$$

given by $\widehat{\mathbf{u}}$. Since for any control law $\mathbf{u}$ that is not the optimal control law, and for some small time increment h , then it must follow that:

$$\widehat{\mathcal{J}}(t, X_t^{\widehat{\mathbf{u}}}, \widehat{\mathbf{u}}) \geq E_{t,x} \left\{ \int_t^{\bar{t}+h} F(s, X_s^{\mathbf{u}}, \mathbf{u}_s) ds \right\} + \widehat{\mathcal{J}}(t+h, X_{t+h}^{\widehat{\mathbf{u}}}, \widehat{\mathbf{u}}) \quad (\text{J.6})$$

where the equality holds only if $\mathbf{u} = \widehat{\mathbf{u}}$. This expression can be re-written as:

$$-E_{t,x} \left\{ \int_t^{\bar{t}+h} F(s, X_s^{\mathbf{u}}, \mathbf{u}_s) ds \right\} \geq \mathcal{J}(t+h, X_{t+h}^{\widehat{\mathbf{u}}}, \widehat{\mathbf{u}}) - \widehat{\mathcal{J}}(t, X_t^{\widehat{\mathbf{u}}}, \widehat{\mathbf{u}}) \quad (\text{J.7})$$

In the limit as $h \rightarrow 0$, one obtains on the left-hand side:

$$E_{t,x} \left\{ \int_t^{\bar{t}+h} F(s, X_s^{\mathbf{u}}, \mathbf{u}_s) ds \right\} \sim F(t, X_t^{\mathbf{u}}, \mathbf{u}_s) h \quad (\text{J.8})$$

and on the right-hand side:

$$\widehat{\mathcal{J}}(t+h, X_{t+h}^{\widehat{\mathbf{u}}}, \widehat{\mathbf{u}}) - \widehat{\mathcal{J}}(t, X_t^{\widehat{\mathbf{u}}}, \widehat{\mathbf{u}}) \sim \left(\frac{\partial \mathcal{J}}{\partial t} + \mathcal{D}_u(\widehat{\mathcal{J}}) \right) h \quad (\text{J.9})$$

where $\mathcal{D}_u$ is the Dynkin operator (also known as the Itô operator or Kolmogorov backward operator) for stochastic calculus (similar to the remainder terms in a Taylor expansion). A full expansion of the Dynkin operator is given in the section below. Dividing by h then gives:

$$F(t, X_t^{\mathbf{u}}, \mathbf{u}) + \frac{\partial \mathcal{J}}{\partial t} + \mathcal{D}_u(\widehat{\mathcal{J}}) \leq 0 \quad (\text{J.10})$$

By definition, if $\widehat{\mathbf{u}}$ is the optimal control law, then it will give equality in the above expression. Therefore, $\widehat{\mathbf{u}}$ must be the control law that maximizes the left-hand side above. That

is, J satisfied the Hamilton-Jacobi-Bellman (HJB) equation:

$$\frac{\partial \mathcal{J}}{\partial t} + \sup_{\mathbf{u} \in \mathcal{U}} \left\{ F(t, X_t, \mathbf{u}) + \mathcal{D}_u \left(\widehat{\mathcal{J}} \right) \right\} = 0, \text{ for all } (t, x) \in (0, T) \times R^n \quad (\text{J.11})$$

$$\widehat{\mathcal{J}}(T, x) = \Phi(x), \text{ for all } x \in R^n \quad (\text{J.12})$$

The supremum in the HJB equation above is obtained for each $(t, x) \in [0, T] \times R^n$ by $\mathbf{u} = \widehat{\mathbf{u}}(t, x)$.

J.3 Dynkin operator or Ito formula

Here the Dynkin operator (also known as the $\text{It}\widehat{o}$ operator, or Kolmogorov backward operator) is derived for stochastic differential equations that have both a Wiener process (Gaussian) drift component and a Poisson random event-driven component (see Belavkin, 1993).

Given a function $f(t, X, \mathbf{u})$ of a stochastic process X , then X is given by:

$$dX_t = \mu(t, X_t, \mathbf{u}(t, X_t)) dt + \sigma(t, X_t, \mathbf{u}(t, X_t)) dW_t + \xi(t, X_t, \mathbf{u}(t, X_t)) dY_t \quad (\text{J.13})$$

where $\mu(t, X_t, \mathbf{u}(t, X_t)) \in R^n$ is a deterministic influence, $W \in R^n$ is a Wiener process whose variance is scaled by $\sigma(t, X_t, \mathbf{u}(t, X_t)) \in R^{n \times d}$ at time t , $\xi(t, X_t, \mathbf{u}(t, X_t)) \in R^{n \times l}$ is a random variable, and $Y \in R^l$ is a Poisson process marked by a magnitude $\xi(t) \in R^{n \times l}$ that may also be a random variable and that is a function of t .

For 1-dimensional processes, the differential of f is calculated:

$$df = \frac{\partial f}{\partial x} dx + \frac{1}{2} \frac{\partial^2 f}{\partial x^2} (dx) \quad (\text{J.14})$$

$$= \frac{\partial f}{\partial x} (\mu dt + \sigma dW) + (f(x + \xi) - f(x)) dY + \quad (\text{J.15})$$

$$\frac{1}{2} \frac{\partial^2 f}{\partial x^2} \left((\mu dt)^2 + (\sigma dW)^2 + (\eta \xi dY)^2 + 2\mu\sigma dt dW + 2\mu\eta \xi dY dt + 2\sigma\eta \xi dW dY \right) \quad (\text{J.16})$$

On the right-hand side in term A, since the Poisson process is a jump process, the differential is not continuous, so it must be expressed as a finite difference that occurs with the probability of $E(Y)$. On the last line, terms I, IV, V, and VI may be neglected, since $(dt)^2 \sim dt dW \sim dW dY \ll dt$. In term II, dW^2 is of the order of dt , since the expected value of dW^2 is the same as $\text{var}(dW)$, which is dt for a Wiener process, so the term can be replaced by $\sigma^2 dt$. In term III, $dY^2 = dY$. Thus, rearranging terms to separate deterministic and stochastic components gives:

$$df = \left(\frac{\partial f}{\partial x} \mu + \frac{1}{2} \frac{\partial^2 f}{\partial x^2} \sigma^2 \right) dt + \frac{\partial f}{\partial x} \sigma dW + (f(x + \xi) - f(x)) dY \quad (\text{J.17})$$

For use in the HJB equation, the stochastic components of this equation must have expected values of zero. Set $d\zeta = dY - E(Y) dt$, which has mean zero. For term A in J.17, add and subtract $E\{(f(x + \xi) - f(x)) dY\} = E\{(f(x + \xi) - f(x))\} E\{dY\} = E\{(f(x + \xi) - f(x))\} E(Y) dt$, since the two factors are independent. Now define a new shot noise term, $d\zeta = dY - E(Y) dt + E(Y) dt$, which has an expected value of zero. Inserting

these terms into J.17 and rearranging, one obtains:

$$\begin{aligned}
df = & \left(\frac{\partial f}{\partial x} \mu + \frac{1}{2} \frac{\partial^2 f}{\partial x^2} \sigma^2 + E(Y) E\{f(x + \xi) - f(x)\} \right) dt \\
& + \frac{\partial f}{\partial x} \sigma dW + (f(x + \xi) - f(x)) d\zeta_A + E(Y) (f(x + \xi) - f(x) - E[f(x + \xi) - f(x)]) dt
\end{aligned} \tag{J.18}$$

The above expression has Wiener and Poisson stochastic components with zero means, and an exponential random term that goes to zero as $dt \rightarrow 0$. In Equation J.17, the coefficient for dt in the first term on the right-hand side is the Dynkin operator, $\mathcal{D}$, or Itô operator for the function f of stochastic variable X :

$$\mathcal{D}(f) = \frac{\partial f}{\partial x} \mu + \frac{1}{2} \frac{\partial^2 f}{\partial x^2} \sigma^2 + E(Y) E\{f(x + \xi) - f(x)\} \tag{J.19}$$

Expressed in multivariate form, this is:

$$\begin{aligned}
\mathcal{D}(f) = & \sum_{i=1}^n \mu_i(t, x) \frac{\partial f}{\partial x_i}(x) + \frac{1}{2} \sum_{i=1}^n \sum_{j=1}^n C_{ij}^2(t, x) \frac{\partial^2 f}{\partial x_i \partial x_j}(x) \\
& + \sum_{i=1}^n \sum_{k=1}^l E(Y_{i,k}) E\{f(x_i + \xi_i) - f(x_i)\} \tag{J.20}
\end{aligned}$$

where the elements of $C^2 = \sigma \sigma'$ are $c_{ij}^2(t, x) = \sigma_i(t, x) \sigma_j(t, x)$.