

# An ecological evaluation of Eagleson's optimality hypotheses

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## Summary

1. The pioneering work of Peter Eagleson has been proposed as a theoretical basis for ecohydrology. Central to the theory are three 'ecological optimality hypotheses' which represent ecologically important aspects of atmosphere–soil–vegetation interactions.
2. The model and its underlying assumptions have never been evaluated in an explicitly ecological context. We examine each of the three optimality hypotheses in turn and test the ability of the model to make ecologically relevant predictions using climate, soil and vegetation data from a semi-arid woodland site in central New Mexico, USA.
3. We find that all three of the optimality hypotheses are ecologically flawed. While we could qualitatively reproduce previously published results, model behaviour under novel conditions was highly variable and frequently unrealistic.
4. The poor performance of the model was probably due to the inadequate treatment of water-limited transpiration in its original derivation. The theory thus requires re-development for ecological application, and we suggest several strands of research that could contribute to its improvement.

*Key-words:* ecohydrology, piñon–juniper woodland, semi-arid vegetation, water balance, Los Piños Mountains

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## Introduction

The development of a quantitative theory of coupled atmosphere–soil–vegetation dynamics is a fundamental ecological and hydrological problem. Such a theory is essential for understanding the global distribution of biomes and their correlation with climate patterns (Holdridge 1947; Stephenson 1990), and the regular changes in vegetation structure and composition observed along topographic and other gradients in microclimate (Whittaker 1967). It is also a key to parameterizing the land–surface boundary conditions of general circulation models (Betts 1999; Desborough 1999) and predicting ecosystem responses to disturbance and climate change (Neilson 1995; Daly *et al.* 2000).

In water-limited ecosystems, atmosphere–soil–vegetation dynamics can be framed as a water-balance problem. Plant growth is limited by the availability of water, which is mediated by a combination of soil properties, precipitation and evaporative demand, and the presence of plants themselves. In this context a recent review (Hatton *et al.* 1997) called for a re-examination of the pioneering work of Peter Eagleson and colleagues (Eagleson 1978a, b, c, d, e, f, g, 1982;

Eagleson & Tellers 1982; Eagleson & Segarra 1985) as the potential basis of an ecohydrological theory of atmosphere–soil–vegetation interactions. Here our goal is to examine critically the theoretical foundation and operational utility of Eagleson's framework in an ecological context. We ask whether the ideas represented in the theory make ecological sense, and whether the model produces fruitful predictions and fundamental insights.

## EQUILIBRIUM WATER BALANCE AND THE ECOLOGICAL OPTIMALITY HYPOTHESES

Eagleson's model uses a statistical–dynamical representation of soil-moisture dynamics, integrated over intermittent precipitation events, to derive analytically the equilibrium partitioning of precipitation into runoff and evapotranspiration. The two surface fluxes depend on 13 parameters (Table 1), all of which can be measured or estimated, as well as the soil moisture concentration,  $s$ . The distribution of storm depths and interstorm periods provides the boundary conditions for equations describing runoff and evapotranspiration. Because the surface fluxes depend on soil moisture concentration, the equilibrium soil moisture concentration  $s_0$ , which represents the spatially and temporally averaged state of the soil, acts as a state variable. The system state and the expected values of annual

**Table 1.** Parameters of Eagleson's water-balance model\*

Parameter	Units	Description
$e_p$	cm day <sup>-1</sup>	Average bare soil potential evaporation rate
$mP_A$	cm	Average annual precipitation
$m_R$	days	Mean storm duration
$m_\tau$	days	Mean rainy season length
$\alpha$	day <sup>-1</sup>	Reciprocal mean time between storms
$\kappa$		Parameter, gamma distribution of storm depths
$\lambda$	cm <sup>-1</sup>	Parameter, gamma distribution of storm depths
$K(1)$	cm day <sup>-1</sup>	Saturated soil hydraulic conductivity
$\psi(1)$	cm	Saturated soil matrix potential
$c$		Soil pore disconnectedness index
$n$		Soil porosity
$h_0$	cm	Surface retention capacity
$k_V$		Vegetation transpiration coefficient
$M$		Fractional canopy density

\*Eagleson 1978a, b, c, d, e, f, g, 1982.

runoff and evapotranspiration are then found by averaging over the entire distribution of boundary conditions and solving the equilibrium:

$$E[P_A] = E[ET_A(s_0, \text{climate, soil, vegetation})] + E[R_A(s_0, \text{climate, soil})] \quad \text{eqn 1}$$

where  $P_A$  is annual precipitation,  $ET_A$  is annual evapotranspiration,  $R_A$  is annual runoff (groundwater and surface water), and  $E[\ ]$  denotes the expected value. We provide a more detailed description of the model below, and a full published derivation is available (Eagleson 1978a, b, c, d, e, f, g, 1982; Eagleson & Tellers 1982; Eagleson & Segarra 1985).

The analytical form of Eagleson's model contrasts with both process-based simulation models (Running & Coughlan 1988; Running & Gower 1991; Neilson 1995; Haxeltine *et al.* 1996) and correlative methods (Stephenson 1998; Iverson & Prasad 2002) for examining vegetation–climate relationships. Like the former, it utilizes mechanistic representations of hydrological processes. However, instead of numerically intensive simulation, Eagleson's statistical–dynamical approach uses probability distributions of climatic parameters to derive equilibrium distributions of hydrologic fluxes, given the necessary vegetation and soil parameters. One advantage of this theoretical approach is that it can be inverted; given the distribution of hydrological responses to precipitation, researchers can derive properties of the soil–vegetation system. Additionally, the analytical and probabilistic nature of Eagleson's theory significantly reduces the system parameterization, relative to most numerical simulations, and thus eases both sensitivity analyses and the generation and testing of hypotheses.

However, several of the below-ground model parameters are still difficult to estimate. Eagleson (1982) eliminated the need to measure them directly by imposing three new constraints on the model, termed the 'ecological optimality hypotheses', which represent a hierarchy of ecological processes that affect water-balance

dynamics on time-scales from years (plant growth and demography) to millennia (soil evolution). While these constraints simply ease parameter estimation for hydrologists (Eagleson 1982; Chavez *et al.* 1994), they allow ecologists to use model output to make explicit predictions concerning the expected state of vegetation in an undisturbed, water-limited system. The three hypotheses are not assumptions that underlie model calculations. Instead, they are *post hoc* constraints that limit the allowable parameter space of the model. However, because of their importance for any ecological application of the model, we examine each hypothesis in turn.

#### CANOPY STRESS MINIMIZATION

According to the first hypothesis, over short time-scales (a few plant generations) the vegetation canopy density ( $M$ ) will equilibrate with the climate and soil parameters to minimize the water stress of the component plants, which Eagleson (1982) equated with a maximization of the equilibrium soil moisture,  $s_0$ . Within the model this constraint corresponds to a minimization of evapotranspiration,  $ET_A$ , with respect to canopy density,  $M$ , to yield the optimal canopy density,  $M_0$  (Eagleson 1982).

The assumption of an equilibrium between a vegetation canopy and water supply is ecologically reasonable, e.g. the hydrological equilibrium of leaf area index (Grier & Running 1977; Larcher 1995). However, it is unlikely that this condition corresponds to a minimization of evapotranspiration, as hypothesized by Eagleson. This assumption is difficult to justify in an ecological and evolutionary context. The major components of plant fitness – development, survival, and fecundity (Crawley 1997) – all require photosynthesis and thus transpiration. Maximizing equilibrium soil moisture in a water-limited system also leaves the limiting resource available to competitors (Tilman 1982), while minimizing evapotranspiration effectively minimizes photosynthetic productivity. Because soil moisture is both a limiting resource and a buffer against stress, it seems most realistic to consider the situation as a trade-off, with the competitive benefits of plant transpiration (e.g. growth and reproduction) balanced against the mortality costs of stress (Tilman 1988; Ehleringer 1993; Tyree *et al.* 1994; Richards *et al.* 1997; Schwinning & Ehleringer 2001).

The first optimality hypothesis is often interpreted as a growth–stress trade-off (MacKay 2001), and Eagleson acknowledges this point of view in later work (Eagleson 1994), but the trade-off is not reflected in any published form of the ecological optimality hypotheses, including Hatton *et al.*'s (1997) review. Part of the problem is the need to incorporate a quantitative measure of stress into the model. In this regard, some recent ecohydrological research utilizing an approach similar to Eagleson's, but explicitly incorporating water stress, seems quite promising (Rodriguez-Iturbe *et al.* 1999).

## SUCCESSIONAL STRESS MINIMIZATION

The second optimality hypothesis predicts that over successional time (many plant generations) species turnover driven by repeated drought will generate an optimal equilibrium community composition whose transpiration efficiency ( $k_{V0}$ ) maximizes the equilibrium soil moisture,  $s_0$ , again under the assumption that soil moisture acts primarily as a buffer against drought stress. Mathematically, as above, this is accomplished by minimizing the total evapotranspiration,  $ET_A$ , this time with respect to the vegetation transpiration coefficient  $k_V$  (Eagleson 1982).

The hypothesis that a plant community that utilized less of the limiting resource could replace a community that used more directly contradicts most theoretical and empirical work on the successional dynamics of plant communities (Bazzaz 1979; Tilman 1988). Instead, most ecologists assume that productivity converges on a rate that balances the supply rate of the limiting resource (Tilman 1988; Enquist & Niklas 2001). Because soil moisture is the limiting resource here, this assumption implies that the system would evolve to minimize the equilibrium soil moisture, the opposite of Eagleson's hypothesis. As in the case of the first optimality hypothesis described above, the community dynamic may be better considered a trade-off between production and drought stress (Breshears & Barnes 1999; Rodriguez-Iturbe *et al.* 1999; Wainwright *et al.* 1999).

However, there are also technical problems with the application of the second hypothesis in the equilibrium water-balance model which render moot further discussion of its conceptual basis. As pointed out by Salvucci (1992), for a given canopy density,  $M$ , the equilibrium soil moisture increases monotonically as the transpiration coefficient,  $k_V$ , decreases. Thus the maximum equilibrium soil moisture corresponds to a vanishingly small  $k_V$ , i.e. no transpiration, no photosynthesis. Together with the ecological concerns, this technical problem suggests that the second optimality hypothesis should be discarded. This conclusion echoes that of Salvucci (1992), although it was not mentioned in Hatton *et al.*'s (1997) review.

## MAXIMUM PRODUCTIVITY SOIL

The third optimality hypothesis addresses the coevolution of vegetation and soils over quasi-geological timescales. The hypothesis predicts that vegetation will alter soil properties (saturated hydraulic conductivity,  $K(1)$ , and pore disconnectedness index,  $c$ , specifically) to maximize the optimal canopy density,  $M_0$ , derived from the first optimality hypothesis. The rationale for this hypothesis is that the maximum optimal canopy density maximizes productivity, given the minimum stress constraint of the first optimality hypothesis (Eagleson 1982).

Hatton *et al.* (1997) refer to the maximum optimal canopy density as the 'climatic climax density', thus

drawing parallels with the Clementsian tradition in ecology. However, under Clements's theory the climatic climax is approached over successional time, not over geological time (Clements 1936). Such a long approach to the climatic climax assumes the stability of both vegetation composition (the transpiration coefficient  $k_{V0}$  does not change) and climatic conditions over geological time, which is not in accord with the paleo-record (Delcourt & Delcourt 1984; Webb & Bartlein 1992; Davis & Shaw 2001). The third optimality hypothesis is linked to successional changes through its dependence on the first two optimality hypotheses; the constant transpiration coefficient,  $k_{V0}$ , is derived from the second optimality hypothesis, and the optimal canopy density,  $M_0$ , is derived from the first. Given the questionable basis of the first optimality hypothesis and the biophysical impossibility of the second, as well as a paucity of data capable of evaluating the third hypothesis, it is difficult to evaluate its validity or ecological relevance.

Thus the ecological optimality hypotheses seem untenable from an ecological perspective. However, we emphasize that while the optimality hypotheses might be invalid, Eagleson's model and methods may still provide valuable insights because the model calculations themselves do not depend on the optimality hypotheses. In that spirit, we next explore the equilibrium water-balance model in some detail. We begin with a review of the model. Next, we validate our application of the model using some of Eagleson's published test data. Finally, we explore the model in new contexts using data from a water-limited site in the Los Piños Mountains, New Mexico, USA. Our goal is to understand the range of behaviour exhibited by the model and its sensitivity to the range of conditions possible at our site. The more general rationale of this work, however, is to explore Eagleson's approach as a tool for understanding water-balance limitations on vegetation structure and function. Despite flaws in the ecological optimality hypotheses, Eagleson's approach might provide insights for developing a more general predictive equilibrium theory of atmosphere-soil-vegetation dynamics.

**Materials and methods**

## THE EQUILIBRIUM WATER BALANCE MODEL

As pointed out by Hatton *et al.* (1997), the original derivation of Eagleson's model is extremely complex. Thus we offer only a brief review of the equations describing the surface fluxes, so that the quantitative nature of the solutions to equation 1 becomes clear. While several authors have altered the model to suit their particular applications (Eagleson & Segarra 1985; Salvucci 1992; Chavez *et al.* 1994; Salvucci & Entekhabi 1994), we limit our analysis to the model summarized in the appendix of Eagleson (1982). Note that we have sometimes changed notation slightly for greater clarity. Symbols are defined in Table 1.

The average annual water balance (equation 1) balances mean annual precipitation,  $mP_A$ , against two mean annual surface fluxes, evapotranspiration and runoff. The evapotranspiration component is the sum of bare soil evaporation and transpiration partitioned by the fractional vegetation canopy density,  $M$ :

$$E[ET_A] = \frac{m_N e_p}{\alpha} (1 - M) \beta_S + Mk_V \quad \text{eqn 2}$$

where  $m_N$  is the mean number of rainstorms per year and  $\beta_S$  is the average bare soil evaporation efficiency, derived (Eagleson 1978d) based on intrinsic soil properties and the probability distributions of rain-free intervals (which is when evaporation takes place) and rainfall intensity (which determines soil water available). The evaporation efficiency is given by:

$$\begin{aligned} \beta_S = & \frac{\gamma[\kappa, \lambda h_0]}{\Gamma(\kappa)} - \left[ 1 + \frac{\alpha h_0 / e_p}{\lambda h_0} \right]^{-\kappa} \\ & \frac{\gamma[\kappa, \lambda h_0 + \alpha h_0 / e_p]}{\Gamma(\kappa)} e^{-BE} + \left\{ 1 + \frac{\gamma[\kappa, \lambda h_0]}{\Gamma(\kappa)} \right\} \\ & \{ 1 - e^{-BE - \alpha h_0 / e_p} [1 + Mk_V + (2B)^{1/2} E - w / e_p] \\ & + e^{-CE - \alpha h_0 / e_p} [Mk_V + (2C)^{1/2} E - w / e_p] \\ & + (2E)^{1/2} e^{-\alpha h_0 / e_p} [\gamma(3/2, CE) - \gamma(3/2, BE)] \} \\ & + \left[ 1 + \frac{\alpha h_0 / e_p}{\lambda h_0} \right]^{-\kappa} \frac{\gamma[\kappa, \lambda h_0 + \alpha h_0 / e_p]}{\Gamma(\kappa)} \\ & \{ (2E)^{1/2} [\gamma(3/2, CE) - \gamma(3/2, BE)] \\ & + e^{-CE} [Mk_V + (2C)^{1/2} E - w / e_p] \\ & - e^{-BE} [Mk_V + (2B)^{1/2} E - w / e_p] \} \end{aligned} \quad \text{eqn 3}$$

$$B = \frac{1 - M}{1 + Mk_V - w / e_p} + \frac{M^2 k_V + (1 - M) w / e_p}{2(1 + Mk_V - w / e_p)^2} \quad \text{eqn 4}$$

$$C = 1/2(Mk_V - w / e_p)^{-2} \quad \text{eqn 5}$$

$$E = \frac{\alpha n(c - 3)K(1)\Psi(1)\phi_e}{\pi e_p^2} s_0^{(c+5)/2} \quad \text{eqn 6}$$

where  $w$  is capillary rise and  $\phi_e$  is the exfiltration diffusivity, given by:

$$\phi_e = s_0^{\frac{c+1}{2}} \left[ 1.85 s_0^{-1.85} \int_0^{s_0} s^{\frac{c+1}{2}} [s_0 - s]^{0.85} ds \right] \quad \text{eqn 7}$$

All other parameters are found in Table 1. The notations  $\Gamma()$  and  $\gamma()$  represent the complete and incomplete gamma functions, respectively. The similarly derived runoff component (Eagleson 1978e) is given by:

$$E[R_A] = mP_A \left( e^{-G-2\sigma} \Gamma(\sigma + 1) \sigma^{-\sigma} + \frac{m_i K(1)}{mP_A} s_0^c \right) \quad \text{eqn 8}$$

where

$$G = \left[ K(1) \frac{m_N m_R}{mP_A} \right] \left[ \frac{(1 + s_0^c)}{2} - w / K(1) \right] \quad \text{eqn 9}$$

$$\sigma = \left[ \frac{5n(c - 3)\lambda^2 K(1)\Psi(1)\phi_i m_R}{12\pi\kappa^2} \right]^{1/3} (1 - s_0)^{2/3} \quad \text{eqn 10}$$

and  $\phi_i$  is the infiltration diffusivity given by:

$$\phi_i = (1 - s_0)^{5/3} \int_{s_0}^1 s^{\frac{c+1}{2}} [s - s_0]^{2/3} ds \quad \text{eqn 11}$$

Note that equation 8 corrects a typographical error in Eagleson (1982), where  $K(1)$  was erroneously replaced with the saturated intrinsic permeability,  $k(1)$ . The error was found via dimensional analysis, and was subsequently validated against the original derivation (Eagleson 1978g). Following Eagleson, we assumed no capillary rise ( $w = 0$ ) and a small, constant value for surface retention capacity ( $h_0 = 0.1$ ).

We explored the model by using canopy density,  $M$ , as a state variable in addition to the equilibrium soil moisture,  $s_0$ ; for a given set of climate, soil and vegetation parameters we found combinations of  $M$  and  $s_0$  values that satisfy equation 1. We selected these particular state variables because they are directly observable phenomena and thus make the behaviour of the model more intuitively meaningful, and because they represent the ecological aspect of the model by coupling vegetation changes directly to changes in soil moisture. All calculations were performed using MATLAB.

#### MODEL VALIDATION

To ensure that the model was coded correctly and functioning properly, we used parameters for two contrasting sites and four representative soil types (Table 2) that were used in the original development and testing of the equilibrium water-balance model (Eagleson 1978a, b, c, d, e, f, g, 1982). However, it is important to note that some uncertainty exists, as in the original presentation, because different publications include both alternative parameter values and approximations for several equations that we use here. Thus we are able only to make qualitative, graphical comparisons of our results with those published by Eagleson.

#### LOS PIÑOS SITE DESCRIPTION AND PARAMETER ESTIMATION

Our study site is a semi-arid woodland located on the slopes of the Los Piños Mountains, New Mexico, USA, within the Sevilleta National Wildlife refuge (34°21' N latitude, 106°32' W longitude, mean elevation 1919 m). The Los Piños site is dominated by Colorado piñon (*Pinus edulis*, Engelm.) and one-seed juniper [*Juniperus monosperma* (Engelm.) Sarg.], interspersed with grass, forbs and bare soil. Because tree canopy density is

**Table 2.** Parameter values for two sites used by Eagleson\*: climate and soil

Parameter	Units	Location			
		Clinton, MA		Santa Paula, CA	
$mP_A$	cm	111.3		54.4	
$e_p$	cm day <sup>-1</sup>	0.15		0.27	
$m_R$	days	0.32		1.4	
$m_B$	days	3.0		10.4	
$m_\tau$	days	365		212	
$\kappa$		0.5		0.25	
$k_V$		1.0		1.0	

Parameter	Units	Soil			
		Clay	Clay loam	Silt loam	Sandy loam
$n$		0.45	0.35	0.35	0.25
$c$		12	10	6	4
$K(1)$	cm day <sup>-1</sup>	0.72	2.0	8.64	18
$\psi(1)$	cm	25	19	166	200

\*Eagleson 1978a, b, c, d, e, f, g, 1982.

constrained by local water-balance conditions (Kerkhoff *et al.* 2003), the site is ideal for a test of the model, given the appropriate parameters. We derived values for climate, soil and vegetation parameters (Table 3) from the Sevilleta Long-term Ecological Research (LTER) program data archives.

Soil parameters were derived from published descriptions (Johnson 1988) using equations (Rawls & Brakensiek 1982) that relate model soil hydraulic parameters (Brooks & Corey 1966) to the porosity values and sand and clay content estimates in the soil descriptions. We selected four soils that represent the range of variation found at the site (Table 3).

Climate parameters were estimated from the Sevilleta LTER meteorological record. For a related project

**Table 3.** Parameter estimates for the Los Piños woodland site: climate (numbers in bold vary between climate scenarios); soil

Parameter	Units	Los Piños			
		minimum	maximum		maximum
$mP_A$	cm	<b>27.5</b>	<b>42.9</b>		
$e_p$	cm day <sup>-1</sup>	<b>0.32</b>	<b>0.47</b>		
$m_R$	days	0.09	0.09		
$m_B$	days	3.17	3.17		
$m_\tau$	days	365	365		
$\kappa$		0.72	0.72		
$k_V$		0.30	0.21		

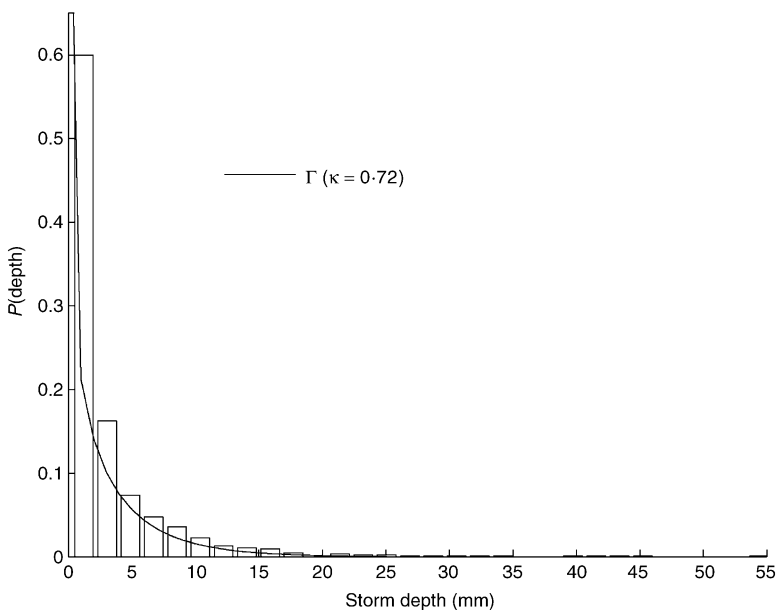
  

Parameter	Units	Soil			
		Soil 1	Soil 2	Soil 3	Soil 4
$n$		0.52	0.47	0.43	0.42
$c$		13.83	17.07	9.32	6.44
$K(1)$	cm day <sup>-1</sup>	0.0028	0.65	0.10	0.083
$\psi(1)$	cm	343.31	52.53	93.33	75.08

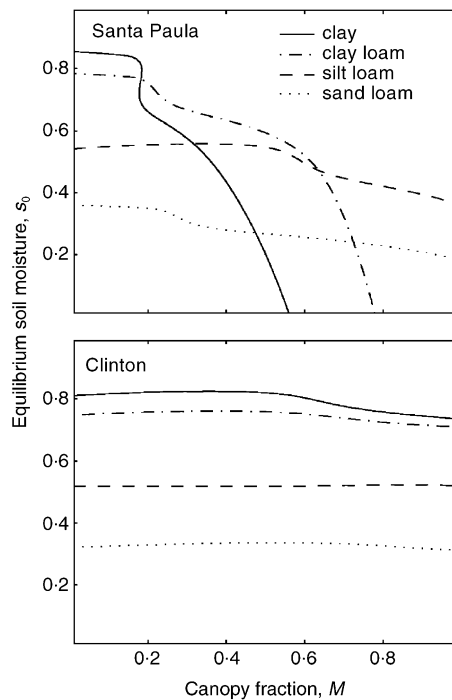
(Kerkhoff *et al.* 2003) we developed spatially distributed estimates of the potential bare soil evaporation rate,  $e_p$ , and mean annual precipitation,  $mP_A$ , using a combination of empirically fitted lapse functions for temperature and precipitation and inverse-distance weighting among the measurements from the different stations. Values for the potential bare soil evaporation rate ( $e_p$ ) were calculated using the Penman equation (Penman 1948). For this project we used the minimum and maximum values of  $e_p$  and  $mP_A$  for the Los Piños site to construct four different climate scenarios.

We drew all temporally dependent precipitation parameters ( $m_R$ ,  $m_B$ ,  $m_\tau$ ,  $\kappa$ ; Table 1), from the 7-year, hourly precipitation time series of the Cerro Montoso weather station, which is centrally located within the Los Piños site (34°21' N latitude, 106°32' W longitude, elevation 1971 m). Thus, in terms of precipitation, the four climate scenarios differ only in their mean annual values, under the assumption that the mean annual differences are accounted for by variation in mean storm depth rather than variation in the temporal parameters. Individual storms were registered in the 7-year (1990–96) record as non-zero rainfall measurements separated by at least 1 h with no measurable precipitation. The gamma distribution (Eagleson 1978b) proved to be an accurate description of the distribution of storm depths (Fig. 1). The assumption of common properties in the temporal distribution of storm events across our climate scenarios probably does not reflect the actual field conditions. However, no other weather station within the study site has been in operation long enough to derive reliable estimates of the temporal precipitation parameters.

Because we treat canopy density as a state variable, the transpiration coefficient,  $k_V$ , is the only vegetation parameter necessary for the model. According to Eagleson's (1982) definition the transpiration coefficient is the ratio of the unstressed transpiration rate to the bare soil potential evaporation rate ( $e_p$ ). We derived maximum transpiration rates for piñon and juniper

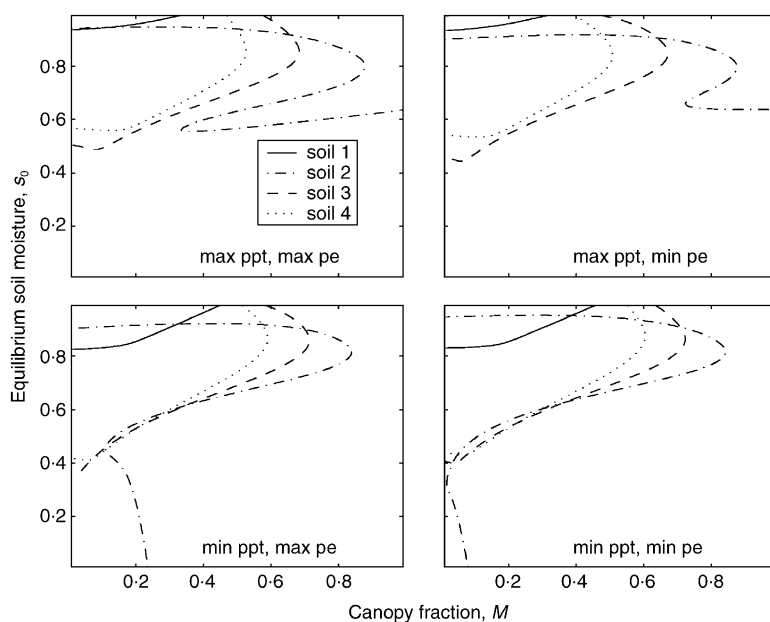


**Fig. 1.** Histogram of storm depths for the Los Piños woodland site, with fitted gamma distribution.



**Fig. 2.** Water-balance solutions using Eagleson's published soil and climate parameters (Table 2). Isoclines represent parameter combinations ( $M$ ,  $s_0$ ) that satisfy equation 1.

from water-use efficiency and maximum net photosynthesis values measured in the field (Barnes 1986). We converted instantaneous transpiration rates ( $\text{cm s}^{-1}$ ) to daily rates by assuming a mean day-length of 12 h. To make a composite measure we simply averaged the values for piñon ( $0.083 \text{ cm day}^{-1}$ ) and juniper ( $0.110 \text{ cm day}^{-1}$ ). The transpiration coefficient,  $k_{\text{tr}}$ , for each climate scenario was then calculated by dividing the composite unstressed transpiration rate ( $0.097 \text{ cm day}^{-1}$ ) by the corresponding  $e_p$  value.



**Fig. 3.** Water-balance solutions for the Los Piños woodland site parameters (Table 3). Isoclines represent parameter combinations ( $M$ ,  $s_0$ ) that satisfy equation 1.

## Results

### MODEL VALIDATION

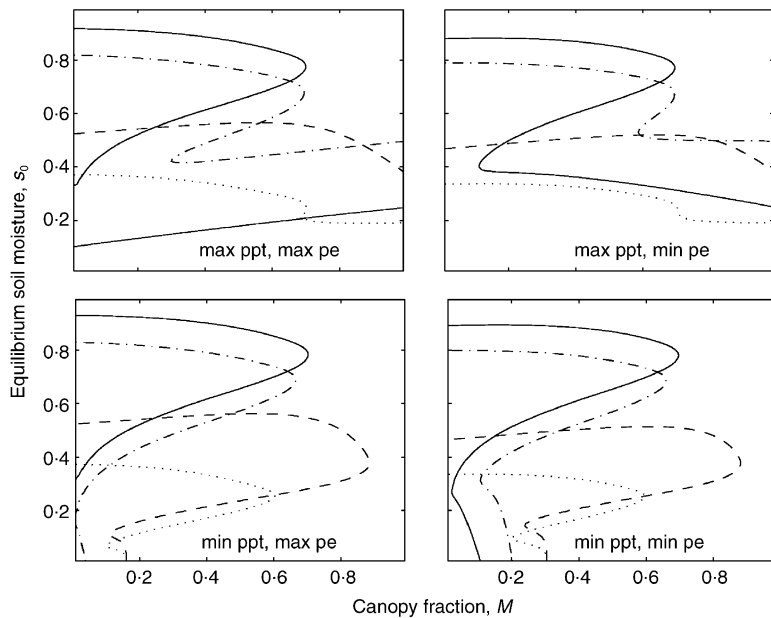
We were able to recreate Eagleson's results qualitatively for the Santa Paula and Clinton sites and for the four soils (Fig. 2). However, a few notable differences were present despite our use of the published parameter values. Importantly, Eagleson's development of the first ecological optimality hypothesis was predicated on the presence of an intermediate value of  $M$  that produces the maximum equilibrium soil moisture. While his results depicted such unimodal solution isoclines (e.g. Eagleson 1982, Fig. 4), our results for Santa Paula show only one soil reaching a maximum  $s_0$  at a non-zero value of  $M$ . Our results for Clinton are more similar to Eagleson's, including the occurrence of unimodal isoclines, although his isocline for the clay soil decreased more steeply at high  $M$ . Reasons for these small discrepancies remain unclear, but may include parameter uncertainties mentioned above, and differences in the numerical methods used to generate the isoclines. Nevertheless, the qualitative agreement between our results and the original graphs implies that the model is coded properly.

### MODEL EXPLORATION: LOS PIÑOS SITE

Using the Los Piños parameters, model behaviour was remarkably variable and quite different from any previously published results (Fig. 3). The solution isoclines ranged from monotonically increasing (soil 1), to hysteretic (soil 2), to more complicated (soils 3 and 4). While variation in climate parameters had an effect on the resulting water balance isoclines, solutions for each soil were relatively similar in the four scenarios.

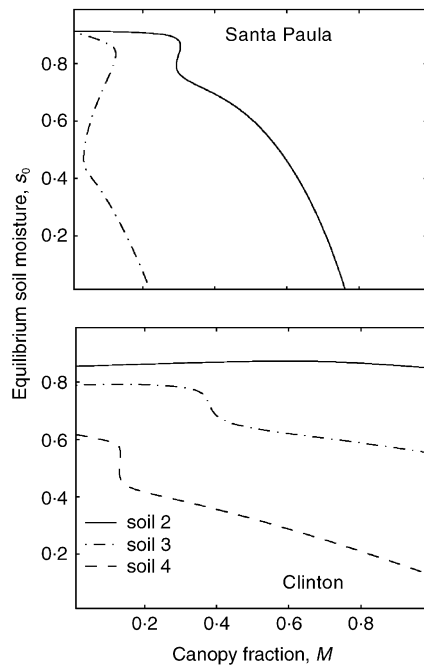
The first ecological optimality hypothesis (minimum stress canopy) assumes the existence of a unique  $s_0$  value for a given canopy density. For our results, this assumption frequently did not hold. In most cases water-balance solutions involved equilibrium soil moisture values above 0.4, despite the arid site conditions. Hourly field soil moisture measurements made using time-domain reflectometry at two weather stations within the Los Piños site in 1999 averaged 0.15, with a maximum value of 0.3 shortly after a storm event (Sevilleta LTER, unpublished results).

To make sure our results did not arise from an idiosyncratic and unrealistic combination of parameter estimates, we reciprocally exchanged our soil and climate parameters (Table 3) with Eagleson's (Table 2). That is, we made water-balance calculations using his soil parameters in the four Los Piños climate scenarios, and using the Los Piños soil parameters in the Clinton and Santa Paula climates. The results for the Los Piños climate (Fig. 4) exhibited variability consistent with our original results, which suggested that the arid nature of the climate, rather than the soil, is responsible for the unusual behaviour of the model. Likewise,



**Fig. 4.** Water-balance solutions for the Los Piños climate parameters (Table 3) with Eagleson's soil parameters (Table 2). Isoclines represent parameter combinations ( $M$ ,  $s_0$ ) that satisfy equation 1.

when the Los Piños soils were subjected to the Santa Paula and Clinton climates, they behaved in greater accord with previously published results (Fig. 5). However, under each climate at least one of the soils produced no solution – no combination of parameters satisfied equation 1. In all cases the surface fluxes ( $ET_A$  and  $R_A$ ) exceeded annual precipitation for all parameter values.



**Fig. 5.** Water-balance solutions for Eagleson's climate parameters (Table 2) with the Los Piños soil parameters (Table 3). Isoclines represent parameter combinations ( $M$ ,  $s_0$ ) that satisfy equation 1.

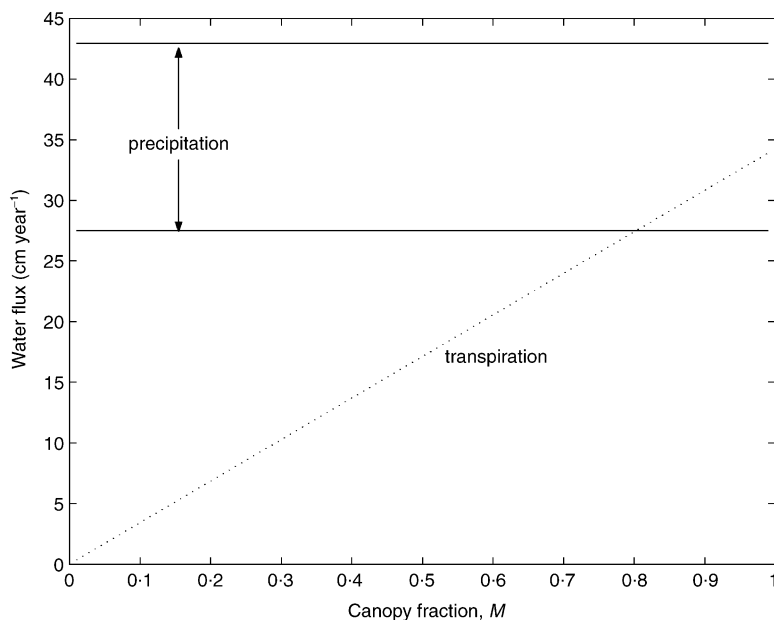
## Discussion

Our study shows that the Eagleson water-balance model displays a wider range of behaviour than previously published results have indicated. Three aspects of our results should be of particular concern for ecohydrologists interested in using Eagleson's approach. First, under arid conditions the pattern of water-balance solutions becomes very complicated and perhaps unrealistic, and this result depends only partly on the particulars of the soil parameterization. Second, the equilibrium soil-moisture values found by the model were, in most cases, unrealistically high, regardless of canopy density. Third, the ecological optimality hypotheses cannot be addressed because solutions almost never displayed a unique, intermediate canopy density value that maximized the equilibrium soil moisture. Because the plausibility of the ecological optimality hypotheses has already been thoroughly questioned (see Introduction), we will not discuss the third aspect of our results further, except to say that our results using Eagleson's published parameter values cast further doubt on the utility of the first optimality criterion (maximizing equilibrium soil moisture with respect to canopy density).

The complicated and unrealistic solutions of the model were confined primarily to our new results. The Los Piños parameters represent a climate more arid than in any previously published application of Eagleson's model. However, the model is specifically designed to describe the hydrology of water-limited systems, and woodland ecosystems like the Los Piños site are far from the extremes of aridity found on Earth. Thus our study suggests that the model requires significant modifications to serve as a basic ecohydrological theory.

The most obvious problem is the assumption that transpiration always occurs at the potential (maximum) rate, independent of soil moisture concentration. Under conditions of relatively abundant water this assumption may be sufficient. However, as the degree of water limitation increases the assumption becomes increasingly problematic. In semi-arid woodlands plants may spend much of their time transpiring at reduced rates due to complications associated with water stress (Barnes 1986; Lajtha & Barnes 1991; Lajtha & Getz 1993; Linton *et al.* 1998). Thus, given the assumption that water stress is one of the primary factors structuring water-limited vegetation, it seems to be a critical oversight that transpiration is considered independent of soil moisture concentration.

Furthermore, in the model this assumption can produce situations in which the total amount of water is not conserved. Below a threshold value for annual precipitation, the total annual transpiration flux will exceed the water input, effectively generating water in excess of its availability (Salvucci 1992). This situation occurs at high canopy densities and low precipitation conditions for the Los Piños site (Fig. 6). Because transpiration is independent of soil moisture, and approaches



**Fig. 6.** Annual water flux components, Los Piños climate parameters (Table 3) as a function of canopy density,  $M$ .

(or exceeds) the magnitude of the precipitation input, the fluxes that are sensitive to soil moisture (evaporation and runoff) must take on extremely anomalous values to satisfy equation 1. This probably explains both the unusual trajectories of the solution isoclines under the Los Piños climate and the unrealistically high soil moisture values of the solutions.

To work around this problem, Salvucci & Eagleson (1992) limit transpiration to periods spent above a threshold soil moisture concentration. While their derivation makes intuitive sense, it assumes that plants are either transpiring (i.e. at their maximum) or not, rather than chronically transpiring at a reduced rate, as is likely at our site (Barnes 1986; Lajtha & Barnes 1991; Lajtha & Getz 1993; Linton *et al.* 1998). However, when we added their modifications to the water-balance model our results for the Los Piños site did not change. Another potential remedy has been proposed (Huang *et al.* 2001), but it requires additional vegetation parameters and the details of its implementation are unclear. What is clear is that the model must integrate more fully the dynamics of transpiration if it is to capture water-balance dynamics accurately under even moderate water limitation.

Because dynamic transpiration would require the addition of at least one more vegetation parameter (e.g. critical leaf water potential), it would also allow for a more realistic description of plant water stress and the investigation of the potential impacts of fitness trade-offs. For example, Schwinning & Ehleringer (2001) found that the optimal suite of phenotypic characters related to water use in plants depends on the temporal and spatial pattern of soil moisture availability. Importantly, different plant phenotypes exhibited very different transpiration responses to soil drying and episodic

precipitation inputs. Incorporating physiological differences among plant functional types and the trade-offs that reinforce phenotypic variation into theories of atmosphere–soil–vegetation dynamics is critical for understanding ecological responses and feedbacks to climate change (Breshears & Barnes 1999; Rodriguez-Iturbe *et al.* 1999; Daly *et al.* 2000).

## Conclusions

We have documented several substantial problems that inhibit ecological applications of Eagleson's model. The three ecological optimality hypotheses, while hydrologically expedient, are ecologically untenable. Further, transpiration is not handled adequately by the model, which can lead to grossly unrealistic results. Nevertheless, the statistical–dynamic basis and analytical form of the equilibrium water balance model provides an important complement to numerical simulations and correlative approaches. Specifically, the addition of physiological realism (e.g. dynamic, moisture-dependent transpiration, stress responses) to ecohydrological theory may reinvigorate the search for new ecological optimality principles (Rodriguez-Iturbe *et al.* 1999). Although the daunting complexity of coupled soil–vegetation–atmosphere systems makes the development of general theory extremely difficult, we agree with Hatton *et al.* (1997) that, '... by pursuing, *redeveloping*, and *extending* [our emphases] ... theory, scientists may learn more about the nature of the problem itself, even if not finding the actual means to solve it.'

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