Ecological Optimality in Water-Limited Natural Soil-Vegetation Systems

2. Tests and Applications

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The long-term optimal climatic climax soil-vegetation system is defined for several climates according to previous hypotheses in terms of two free parameters, effective porosity and plant water use coefficient. The free parameters are chosen by matching the predicted and observed average annual water yield. The resulting climax soil and vegetation properties are tested by comparison with independent observations of canopy density and average annual surface runoff. The climax properties are shown also to satisfy a previous hypothesis for short-term optimization of canopy density and water use coefficient. Using these hypotheses, a relationship between average evapotranspiration and optimum vegetation canopy density is derived and is compared with additional field observations. An algorithm is suggested by which the climax soil and vegetation properties can be calculated given only the climate parameters and the soil effective porosity. Sensitivity of the climax properties to the effective porosity is explored.

INTRODUCTION

Eagleson [this issue] suggested that there may be ecological pressures for change in natural soil-vegetation systems which drive a synergistic development toward a water- or energy-limited equilibrium state in a given climate. Identification of the conditions for this equilibrium should allow a priori specification of one or more of the physical parameters of the soil and vegetation. This would substantially ease the problem of estimating effective land surface parameters when dealing with the hydrothermal fluxes of large natural landsurfaces. Such problems arise continually in catchment hydrology and in the boundary conditions for models of atmospheric dynamics.

The theoretical formulation of these hypotheses is presented in the first paper of this pair [Eagleson, this issue]; here we present some preliminary observational evidence in their support. We close with suggested algorithms for applying the hypotheses where the single free parameter, the soil effective porosity, is determined using observations of either canopy density or average annual streamflow.

REVIEW OF EQUILIBRIUM HYPOTHESES

The one-dimensional water balance model of Eagleson [1978a-g] is written in terms of five surface parameters: the vegetation canopy density $M$, the species-dependent plant water use coefficient $k_0$, the soil effective porosity $n_e$, the saturated intrinsic permeability $k(1)$, and the soil pore disconnectedness index $c$. The analytical structure of this model is summarized in an appendix to the first paper of this pair [Eagleson, this issue].

Eagleson argues that where water is limiting, the short-term ecological pressure will be to minimize water demand stress through adjustment of both canopy density and plant species so that the soil moisture is maximized. For a given climate and soil, this is written

$$\left( \frac{\partial s_0}{\partial M} \right)_{k_0} = 0 \quad M = M_0 \quad (1)$$

where $s_0$ is the average soil moisture concentration in the root zone; $M_0$ is the short-term equilibrium canopy density; $k_0$ is the short-term equilibrium plant coefficient.

Eagleson shows that (1) and (2) lead to the more convenient expressions of this equilibrium:

$$\left( \frac{\partial E_T}{\partial M} \right)_{k_0} = 0 \quad M = M_0 \quad (3)$$

$$\left( \frac{\partial E_T}{\partial k_0} \right)_{M} = 0 \quad k_0 = k_{0_0} \quad (4)$$

where $E_T$ is the average annual evapotranspiration.

Equations (3) and (4) define the 'complete vegetal equilibrium' curve of Figure 1. For canopy densities $M_0 > 0.42$, complete equilibrium is not possible by this definition because (2) cannot be satisfied.

In moist climates where energy limits, Eagleson [this issue] reasoned that the pressures for maximization of soil moisture are weakened with respect to the species and the pressure shifts to maximization of biomass productivity. He hypothesized that for a given moist climate and soil the canopy will always satisfy (1) and that maximization of a given species' biomass leads to

$$\left( \frac{\partial M_0}{\partial E} \right)_{k_0} = 0 \quad (5)$$

where $E$ is a dimensionless climate-soil parameter that is directly proportional to $S_0(1-50^2)$ and inversely proportional to $\bar{e}_n$. Here $\bar{e}_n$ is the average potential rate of evaporation from bare soil.

Equation (5) is given in Figure 1 as the line marked 'maximum biomass for given species.' The other parameters...
of Figure 1 are \( h_0 \), the water retention capacity of surface; \( \alpha \), the reciprocal of average time between rainstorms; and \( w \), the rate of capillary rise from water table to surface.

Noticing (as in Figure 2) that in a given climate and for fixed \( k_w \) and \( n_e \), the minimum stress canopy density \( M_0 \) is maximum for a particular set of soil properties \( c \) and \( k(1) \), Eagleson [this issue] hypothesized a long-term soil-vegetation equilibrium. He reasoned that by virtue of additions of organic matter to the soil, the vegetation canopy modifies the soil properties over time in a synergistic development that drives the system once again toward the maximum biomass productivity, \( B_p \). Since this is proportional to canopy water use, we can say

\[
B_p \sim M_0 k_w \delta_a
\]

For constant climate and constant \( k_w \), (6) will maximize where \( M_0 \) has its maximum value \( M_0^* \). The conditions for this equilibrium are then

\[
\left( \frac{\partial M_0}{\partial c} \right)_{k(1)} = 0 \quad M_0 = M_0^* \quad (7)
\]

\[
\left( \frac{\partial M_0}{\partial k(1)} \right)_{c} = 0 \quad M_0 = M_0^* \quad (8)
\]

**The Problem**

The above hypotheses were formulated using a one-dimensional model of the soil moisture fluxes. To test them, one ideally should have direct observations of \( M, k_w, c, k(1) \), and \( n_e \) (in addition to the various climate parameters), from an array of spatially homogeneous natural systems covering a wide range of the dimensionless climate-soil parameter \( E \). In practice, however, at least the soil parameters of natural systems are highly variable, spatially [Nielsen et al., 1973], so even if dense observations of them were available (which is rare), the problem of how to average them areally arises.

We will thus be forced to use indirect spatial averaging of the surface parameters. This is the inverse of the lumped parameter process by which one-dimensional hydrologic models have long been used to explain the behavior of nonhomogeneous landsurfaces. In this inverse or identification process we will seek the values of the soil and vegetation parameters which, when used in the one-dimensional water balance of Eagleson [this issue], best reproduce observed values of the average annual moisture fluxes. Streamflow, wherever it is equivalent to total water yield, is particularly suited to this identification process. In the first place it is a naturally integrated output of the spatially variable system, and additionally, its concentration by the channel network makes it the most easily and most commonly measured of the output moisture fluxes. The equivalence of streamflow and total yield requires that the surface and groundwater catchments are congruent and that the groundwater and surface water runoffs both exit the catchment as streamflow. Of course, there is normally no way of knowing if these conditions are met in a particular case, and the outcome of tests based on the assumption that they are must be uncertain to some degree. We will supplement and check the identification process using limited direct observations of the only readily observable surface parameter, the vegetation canopy density.

**The Data Base**

Three separate data sets are used. The first set contains the two representative contrasting climates of Clinton, Massachusetts and Santa Paula, California used by Eagleson [1978a-g]. These are summarized in the first two columns of Table 1 where

\[
\bar{T}_a \quad \text{average annual atmospheric temperature} ;
\]

\[
m_y \quad \text{average length of rainy season};
\]

\[
m_t \quad \text{average time between rainstorms};
\]

\[
m_r \quad \text{average rainstorm duration};
\]

\[
m_p \quad \text{average annual precipitation};
\]

\[
E[Y_A] \quad \text{average annual water yield (assumed to be equal to average annual streamflow)} ;
\]

\[
k \quad \text{shape factor of gamma-distributed rainstorm depths};
\]

\[
A \quad \text{catchment area}.
\]

Annual precipitation and streamflow observations were published by the U.S. Geological Survey [1940] for the southern branch of the Nashua River near Clinton, Massachusetts. The storm data were taken from U.S. National Weather Service records at Boston, Massachusetts. Streamflow observations on Santa Paula Creek near Santa Paula, California came from U.S. Geological Survey Station 11-1135. Precipitation observations were from Ventura County Flood Control District records. These two catchments are unusual in
that direct visual estimations of vegetation canopy density, made by the authors, are available.

A second data set similar to the first was selected because of the availability of the average annual surface runoff as calculated through empirical separation of streamflow hydrographs [Hoyt et al., 1936] and because of the very large catchment areas involved (9,000-16,000 km²). The upper end of this range is one quarter that of the current grid in atmospheric general circulation models. These data are presented as the last four columns of Table 1, where $E[R_s]$ is the average annual surface runoff. Precipitation data for the Merrimack catchment came from U.S. National Weather Service records at Lowell, Massachusetts and Concord, New Hampshire (annual), and at Boston, Massachusetts (storm). For the Chattahoochee catchment West Point, Georgia and Clayton, Georgia were used. For the Neosho it was Garnett, Kansas and Council Grove, Kansas, while for the James River it was New Canton, Virginia and Roanoke, Virginia.

The third data set was selected with the aim of evaluating the derived relations [Eagleson, this issue, Figure 14] between equilibrium canopy density $M_0$ and average evapotranspiration efficiency $\beta$. Sites were selected to have coordinated observations of vegetation canopy and streamflow and to cover a wide range of the arid-humid climatic spectrum. These data are summarized in Tables 2 and 3. Published descriptions of the land surfaces were used to estimate a range of vegetation canopy density and a range of moist

<table>
<thead>
<tr>
<th>Catchment Number</th>
<th>Location</th>
<th>References</th>
<th>$E[P_s]$, cm</th>
<th>$E[Y_s]$, cm</th>
<th>$E[R_s]$, cm</th>
<th>$M_0$</th>
<th>$E[R_p]$, cm</th>
<th>$\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>W-1</td>
<td>Albuquerque, N.M.</td>
<td>U.S. Department of Agriculture [1967]</td>
<td>11.1</td>
<td>0.51</td>
<td>10.59</td>
<td>0.12-0.15</td>
<td>44.4-40.8</td>
<td>0.24-0.26</td>
</tr>
<tr>
<td>W-2</td>
<td>Cornfield Wash, Colo.</td>
<td>Branson and Owen [1970]</td>
<td>15.98</td>
<td>2.72</td>
<td>13.26</td>
<td>0.16</td>
<td>44.4-40.8</td>
<td>0.30-0.33</td>
</tr>
<tr>
<td>W-3</td>
<td>Tombstone, Ariz.</td>
<td>U.S. Department of Agriculture [1967]</td>
<td>21.97</td>
<td>1.63</td>
<td>20.35</td>
<td>0.35-0.40</td>
<td>37.3-33.7</td>
<td>0.55-0.60</td>
</tr>
<tr>
<td>W-4</td>
<td>Tombstone, Ariz.</td>
<td>U.S. Department of Agriculture [1967]</td>
<td>21.97</td>
<td>0.53</td>
<td>21.44</td>
<td>0.25-0.30</td>
<td>37.3-33.7</td>
<td>0.58-0.64</td>
</tr>
<tr>
<td>W-5</td>
<td>Tombstone, Ariz.</td>
<td>U.S. Department of Agriculture [1967]</td>
<td>21.97</td>
<td>2.77</td>
<td>19.20</td>
<td>0.20-0.25</td>
<td>37.3-33.7</td>
<td>0.52-0.57</td>
</tr>
<tr>
<td>W-6</td>
<td>Flagstaff, Ariz.</td>
<td>Brown [1965]</td>
<td>31.45</td>
<td>1.02</td>
<td>30.43</td>
<td>0.30-0.35</td>
<td>76.2-70.5</td>
<td>0.40-0.43</td>
</tr>
<tr>
<td>W-7</td>
<td>Badger Wash, Colo.</td>
<td>Branson and Owen [1970]</td>
<td>11.91</td>
<td>2.44</td>
<td>9.47</td>
<td>0.13</td>
<td>31.2-28.3</td>
<td>0.30-0.34</td>
</tr>
<tr>
<td>W-8</td>
<td>Santa Paula, Calif.</td>
<td>Eagleson [1978a-g]</td>
<td>11.91</td>
<td>0.89</td>
<td>11.02</td>
<td>0.26</td>
<td>31.2-28.3</td>
<td>0.35-0.39</td>
</tr>
<tr>
<td>W-9</td>
<td>Chickasha, Okla.</td>
<td>U.S. Department of Agriculture [1976]</td>
<td>54.0</td>
<td>17.4</td>
<td>36.6</td>
<td>0.35-0.50</td>
<td>57.9-45.8</td>
<td>0.63-0.80</td>
</tr>
<tr>
<td>W-10</td>
<td>Chickasha, Okla.</td>
<td>U.S. Department of Agriculture [1976]</td>
<td>59.74</td>
<td>2.84</td>
<td>56.9</td>
<td>0.45-0.57</td>
<td>85.8-78.1</td>
<td>0.66-0.73</td>
</tr>
<tr>
<td>W-11</td>
<td>Clinton, Mass.</td>
<td>Eagleson [1978a-g]</td>
<td>111.3</td>
<td>55.4</td>
<td>55.9</td>
<td>0.80-0.95</td>
<td>57.5-52.4</td>
<td>0.97-1.07</td>
</tr>
</tbody>
</table>
TABLE 3. Computation of Catchment Potential Evapotranspiration

<table>
<thead>
<tr>
<th>Catchment Number</th>
<th>$\phi$, $\pi$</th>
<th>$\varepsilon_p$, (annual, lake, cm/d)</th>
<th>$A_s$, (annual), °C</th>
<th>$T_s$, (seasonal), °C</th>
<th>$m_r$, months</th>
<th>$N$</th>
<th>$S$</th>
<th>$q_b$, cal cm$^{-2}$ min$^{-1}$</th>
<th>$A_s$, (seasonal, surface), cm/d</th>
</tr>
</thead>
<tbody>
<tr>
<td>W-1</td>
<td>35</td>
<td>0.411</td>
<td>0.07</td>
<td>13.7</td>
<td>20.9</td>
<td>4</td>
<td>0.37</td>
<td>0.40</td>
<td>0.354</td>
</tr>
<tr>
<td>W-2</td>
<td>35</td>
<td>0.411</td>
<td>0.07</td>
<td>13.7</td>
<td>20.9</td>
<td>4</td>
<td>0.37</td>
<td>0.40</td>
<td>0.354</td>
</tr>
<tr>
<td>W-3</td>
<td>32</td>
<td>0.452</td>
<td>0.075</td>
<td>19.8</td>
<td>28.0</td>
<td>3</td>
<td>0.35</td>
<td>0.45</td>
<td>0.354</td>
</tr>
<tr>
<td>W-4</td>
<td>32</td>
<td>0.452</td>
<td>0.075</td>
<td>19.8</td>
<td>28.0</td>
<td>3</td>
<td>0.35</td>
<td>0.45</td>
<td>0.354</td>
</tr>
<tr>
<td>W-5</td>
<td>32</td>
<td>0.452</td>
<td>0.075</td>
<td>19.8</td>
<td>28.0</td>
<td>3</td>
<td>0.35</td>
<td>0.45</td>
<td>0.354</td>
</tr>
<tr>
<td>W-6</td>
<td>35</td>
<td>0.404</td>
<td>0.070</td>
<td>7.1</td>
<td>8.4</td>
<td>7</td>
<td>0.40</td>
<td>0.52</td>
<td>0.425</td>
</tr>
<tr>
<td>W-7</td>
<td>38</td>
<td>0.244</td>
<td>0.060</td>
<td>11.5</td>
<td>8.8</td>
<td>6</td>
<td>0.50</td>
<td>0.48</td>
<td>0.240</td>
</tr>
<tr>
<td>W-8</td>
<td>34</td>
<td>0.334</td>
<td>0.070</td>
<td>13.8</td>
<td>13.8</td>
<td>7</td>
<td>0.37</td>
<td>0.69</td>
<td>0.323</td>
</tr>
<tr>
<td>W-9</td>
<td>35</td>
<td>0.431</td>
<td>0.070</td>
<td>16.1</td>
<td>21.5</td>
<td>7</td>
<td>0.47</td>
<td>0.67</td>
<td>0.367</td>
</tr>
<tr>
<td>W-10</td>
<td>35</td>
<td>0.334</td>
<td>0.070</td>
<td>13.8</td>
<td>13.8</td>
<td>7</td>
<td>0.47</td>
<td>0.67</td>
<td>0.367</td>
</tr>
<tr>
<td>W-11</td>
<td>42</td>
<td>0.183</td>
<td>0.060</td>
<td>8.4</td>
<td>8.4</td>
<td>12</td>
<td>0.54</td>
<td>0.71</td>
<td>0.220</td>
</tr>
</tbody>
</table>

The bare soil albedo at each site. A range of average seasonal potential evapotranspiration $E[E_{v_p}]$ was then estimated (as described below), using the approximations $k_o = 1$ and $m_r/m_r \gg 1$, as

$$E[E_{v_p}] = m \varepsilon_p$$  (9)

Finally, the average seasonal evapotranspiration $E[E_{v_r}]$ was estimated from the difference between the observed average seasonal precipitation $E[P_s]$ and the observed average seasonal streamflow $E[Y_s]$. The average seasonal evapotranspiration efficiency is then, by definition,

$$\beta = E[E_{v_r}] / E[E_{v_p}]$$  (10)

Potential Rate of Evapotranspiration

In all cases (Tables 1, 2, and 3) the average seasonal rate of bare soil potential evapotranspiration, $\varepsilon_p$, was calculated using Van Bavel's [1966] combination form of the Penman [1948] equation. This is

$$\varepsilon_p = \frac{\bar{q}_b(1 - A_s) - \bar{q}_b + H}{\rho L_e (1 + \gamma/\Delta)} \text{ cm min}^{-1}$$  (11)

where

- $\bar{q}_b$ average seasonal rate of insolation at surface, cal cm$^{-2}$ min$^{-1}$;
- $A_s$ shortwave albedo of moist surface;
- $\rho$ mass density of liquid water, g cm$^{-3}$;
- $L_e$ latent heat of vaporization, 597 cal g$^{-1}$;
- $\gamma/\Delta$ atmospheric parameter, a function of average seasonal atmospheric temperature [Eagleson, 1970, p. 228];
- $c_p$ specific heat of air, cal g$^{-1}$ °C$^{-1}$;
- $R_a$ average atmospheric diffusion resistance [Eagleson, 1970, p. 234], min cm$^{-1}$;
- $\bar{e}_s$ average saturation vapor pressure at atmospheric (screen height) temperature, g cm$^{-1}$ s$^{-2}$;
- $\bar{e}$ average vapor pressure at screen height, g cm$^{-1}$ s$^{-2}$;
- $\Delta$ slope of vapor pressure-temperature curve, g cm$^{-1}$ s$^{-2}$ °C$^{-1}$.

The overbars indicate time-averaged values and result from a zeroth-order time averaging of (9) [Eagleson, 1977].

Assuming the surface to behave as a blackbody with respect to long-wave radiation and approximating the surface temperature by the atmospheric temperature, the average net outgoing longwave radiation can be estimated from [Eagleson, 1977]

$$\bar{q}_b = (1 - 0.8N)(0.245 - 0.145 \times 10^{-10} \bar{R}_a)$$  (13)

cal cm$^{-2}$ min$^{-1}$

where $N$ is the seasonal fractional cloud cover and $\bar{R}_a$ is the average seasonal atmospheric temperature, °K. The average ‘drying power’ $H$ of the atmosphere was evaluated [Eagleson, 1977] from (11) using two sets of average annual evapotranspiration measurements [Jensen and Haise, 1963; Hamon, 1961] at a total of 35 sites from both arid and humid climates. The result, as shown in Figure 3, leads to the empirical expression

$$\bar{q}_b/H = 0.25 + 1/(1 - \bar{S})$$  (14)

where $\bar{S}$ is the average saturation ratio (fractional relative humidity).

When applying these relationships in the present study, the average seasonal surface insolation was estimated from observed lake evaporation [Kohler et al., 1959] using (11), (13), and (14) and a water surface albedo that reflects the latitude $\phi$ of the site. The atmospheric temperature, cloud cover, and saturation ratio were all obtained from U.S. National Weather Service publications and averaged over the rainy season, which is assumed to coincide with the vegetation growing season. The average saturation ratio was estimated using the monthly means of the average 7:30 a.m. and 7:30 p.m. values of $S$. Equations (11), (13), and (14) were
used again to estimate the bare soil potential evaporation rate \( \bar{e}_p \), using published albedo values [Eagleson, 1970, pp. 37] for moist soil.

### The Minimum Stress Canopy Density

The third data set can be used to test the short-term equilibrium hypothesis that the canopy density will adjust itself to minimize stress by maximizing soil moisture. We do this by looking at the useful relationship between average evapotranspiration efficiency \( \beta \) and equilibrium canopy density \( M_0 \). The former is defined as the ratio of the average annual evapotranspiration, \( E[\eta]\) to the average annual potential bare soil evaporation \( E[\bar{e}_p] \). Eagleson [this issue] has derived this relationship, and it is shown here as the solid lines in Figure 4 for various typical values of the plant water use coefficient \( k_v \). The other parameters of Figure 3, \( a h_o/e_p \) and \( w/e_p \), measure the importance to evapotranspiration of surface-retained water and the water table, respectively, and are given nominal values.

Superimposed on the theoretical curves of Figure 4 are the observations of \( M_0 \) and \( \beta \) given in Table 2. The dimensions of the rectangle plotted for each catchment indicate the estimated uncertainty in the variables.

In general the observations are bounded fairly well by the theoretical curves for \( k_v = 1 \) and \( k_v = 0.6 \), although no information is available on the values of the \( k_v \) for the individual catchments. A possible reason for the apparent high evapotranspiration efficiencies for the arid Arizona catchments W-4 and W-5 may be unaged groundwater yield accompanying a low groundwater table. The literature reports that catchment W-10, which is in the same region as W-9, is consistently overgrazed, which may keep its observed canopy density unnaturally low. As was expected, it does seem that the thinner canopies of the drier regions are composed of species having a potential transpiration efficiency (i.e., \( k_v \)) progressively smaller than unity.

The derived \( \beta(M_0) \) relationship appears useful for the estimation of \( \beta \) given observations of the canopy density and species (i.e., \( k_v \)). To facilitate this, the theoretical curves of Figure 4 have been fitted with a third degree Chebyshev polynomial in the range \( 0.1 \leq M_0 \leq 1 \), yielding

\[
\begin{align*}
\beta &= 0.12 + 2.09 M_0 - 1.42 M_0^2 + 0.20 M_0^3 \quad k_v = 1 \\
\beta &= 0.11 + 1.63 M_0 - 0.83 M_0^2 + 0.09 M_0^3 \quad k_v = 0.8 \\
\beta &= 0.12 + 1.08 M_0 - 0.17 M_0^2 - 0.03 M_0^3 \quad k_v = 0.6
\end{align*}
\]

### The Climatic Climax Soil and Vegetation Properties

#### Procedure

The climatic climax soil and vegetation parameters were determined not by direct solution of (7) and (8) but by plotting solutions of the water balance equation in \( c - k(1) \) soil space for successively larger constant values of the minimum stress canopy density \( M_0* \), as is shown in Figure 2. The procedure for doing this had the following steps in a given climate: (1) Fix the values of \( k_v \) and \( n_e \), (2) pick a value of \( M_0 \), (3) pick a value of \( c \), (4) search for the value of \( k(1) \) which satisfies the water balance, (5) repeat 3 and 4 until that \( M_0 \) contour is closed, (6) increment \( M_0 \) and repeat. The peak of the \( M_0* \) "hill" located in this way defines the climatic climax canopy density \( M_0* \) and its associated soil properties \( c \) and \( k(1) \) for the particular fixed values of effective porosity \( n_e \) and plant water use coefficient \( k_v \) in the given climate.

#### Sensitivities

The sensitivity of these climax values of \( k(1) \) and \( c \) to the value of \( n_e \) is explored for the contrasting climates of Clinton, Massachusetts and Santa Paula, California, while keeping the plant coefficient constant at its nominal moist climate value of unity. The results are shown in Figure 5 where the plotted points are each the result of a contour plot such as Figure 2. It is interesting to note that the climax permeability is fairly sensitive both to \( n_e \) within a given climate and to climate at a given \( n_e \). At the same time, the climax disconnectedness index is essentially constant for a given climate, and this value is only slightly sensitive to climate.

The sensitivity of \( M_0* \) to \( n_e \) and \( k_v \) is illustrated in Figure 6. Here, for simplicity, the individual calculated points are not shown. Notice that in the humid (i.e., Clinton) climate, \( M_0* \) is independent of \( n_e \) for large \( k_v \). This says that there is no soil which can produce a canopy density greater than a \( k_v-\)
determined maximum for $k_o > 1$ in a humid climate. This is a reflection of the inverse $M_o - k_o$ relation found by Eagleson [this issue] in climate-controlled situations with $k_o > 1$. In the case of observed complete forest canopies it lends support to the argument of some [Kramer, 1969, p. 338] that $k_o$ never exceeds unity. The increased sensitivity of $M_o^*$ to $k_o$ in the humid as opposed to the arid case is an expression of this same climate limitation.

The shaded areas on Figure 6 represent the range of observed $M_o$ for these catchments as given in Table 2. The sensitivity of $M_o$ to $k_o$ is examined in more detail in Figure 7. The climax value $M_o^*$ is presented for constant $n_e$ in both Clinton and Santa Paula by the solid curve labeled $M_o = M_o^*$. Here again we see the larger sensitivity of the more humid (Clinton) climate. We also see clearly that in both climates there is a limiting value of $k_o$ for a given $n_e$ below which no climax canopy density can be found. This occurs because of the lack of a maximum $S_o$ under these conditions, as was pointed out by Eagleson [this issue, Figure 9]. Also shown in Figure 7 are the two branches of the optimum vegetation hypothesis, as given earlier in Figure 1.

Tests

If the field of $k_v-n_e$ pairs is examined in a given climate, it is possible to pick out the one or more pairs for which some characteristic of the climax state is in agreement with an observation of that characteristic. This has been done for the six catchments of Table 1, using observations of the average annual yield (streamflow). Examples of the resulting array of the climax values are presented in Tables 4 and 5 for the Neosho and Chattahoochee catchments, respectively. In these tables the entered number pairs are $M_o^*$ followed by $E[Y_o]$ as calculated from the Eagleson [1978a–g] water balance model using the climax soil and vegetation properties. The tables were filled in only as necessary to find a soil pair for which the calculated and observed $E[Y_o]$ were approximately equal. These values are in italics. The variations are regular, and the parameter range covered is reasonably exhaustive for the particular climate, so it is unlikely that other solutions exist. The solutions found are summarized for all six catchments in Table 6.

With these values we can go back to Figures 6 and 7 and locate the climax $M_o-\bar{k}_o$ for Clinton and Santa Paula, as shown by the plotted circles. In both figures we see that the points lie squarely within the uncertainty band of the observed canopy density. This serves as limited verification of the climatic climax hypothesis. In Figure 7 we see also that the climatic climax $M_o-\bar{k}_o$ occurs at (for Clinton) or very near (for Santa Paula) the intersection of the short-term vegetal optimum and the long-term climax conditions. This is further
support of the hypothesis [Eagleson, this issue] that the short-term optima are satisfied in the long term.

**The Average Annual Surface Runoff**

**Comparison with Observation**

We also have available the U.S. Geological Survey (USGS) estimates [Hoyt et al., 1936] of the average annual surface runoff $E[R_s]$ at four of the catchments, as seen previously in Table 1. We can compare these surface runoff estimates with the values calculated by the water balance model [Eagleson, 1978a-g] using the climax soil-vegetation properties. Since we have already selected the climax values to fit the total yield, this comparison will perhaps be more a test of Eagleson’s surface runoff function than it will of the climatic climax hypothesis. Nevertheless, in humid climates (Merrimack, James, Chattahoochee) the evapotranspiration, and hence the total yield, are insensitive to soil properties [Eagleson, 1978g, p. 771; Eagleson, this issue, Figure 17], while the partitioning of this total into its surface and groundwater fractions is very sensitive to the soil properties. The comparison, presented first in Table 7, should thus give new information at least for the three humid catchments. Notice in Table 7, that all predictions except that of the dry Neosho catchment are within 10% of the value estimated by the USGS through hydrograph separation. We will have more to say about the Neosho case later.

This same comparison is presented graphically in Figure 8. The solid line in Figure 8 represents Eagleson’s [1978a-g] approximate analytical evaluation of the expected value of the total annual surface runoff. The full form of this function is given in the appendix of the first of these two papers [Eagleson, this issue]. It is written in terms of two dimensionless parameters: $G$, representing the effect of gravity on infiltration, and $\sigma$, representing the effect of capillarity. This general solution results from the analytical approximation of an integral which has been evaluated numerically by Córdova and Bras [1979] for several special cases involving two widely different average soil moisture concentrations. These values are shown by the plotted triangles (wet soil) and squares (dry soil) on Figure 8. Their position above the solid line indicates that the approximate solution consistently underestimates the theoretical runoff. The scatter of the points indicates the presence in the exact solution of one or more additional significant parameters.

The surface runoff values estimated from the observed streamflows by Hoyt et al. [1936] are represented by the plotted circles on Figure 8. Their large scatter and their position with respect to the approximate analytical solution are completely consistent with those of the exact numerical solution, thereby lending support to the theoretical formulation of the surface runoff if not to the approximation being used.

**Sensitivity**

The sensitivity of the predicted surface runoff to variations in the soil properties $k(1)$ and $c$ is shown in Figures 9 and 10, respectively. In these figures the soil properties are varied along orthogonal axes centered on the climax soil properties of the appropriate $M_0$ 'map,' as is illustrated in Figure 2. At each intersection with an $M_0$ contour the appropriate $k(1)$, $c$, $M_0$ are used ($n_0$ and $k_0$ remaining constant) to calculate the values of $\sigma$ and $e^G$. Using the ‘observed’ values of $E[R_s]/m_P$, we can plot the dashed lines in Figures 9 and 10; the range of parameter variation is indicated at the ends of each line. We see from these figures that the surface runoff is insensitive to $c$ but is very sensitive to $k(1)$. The insensitivity to $c$ results from $G$ being insensitive to $c$ for the moderate average soil moistures of these climates. The very large sensitivity to $k(1)$ lends further support to use of the climatic climax hypothesis for parameterization of the soil over very large areas.

This sensitivity to $k(1)$ is responsible for the apparently poorer agreement between observation and theory in Figure 8 compared to that in Table 7. To present the surface runoff function as a unique curve, it was necessary to multiply the dependent variable by the factor $e^G$, which is extremely sensitive to $k(1)$.

**The Soil Pore Disconnectedness Index**

We note in Table 6 that the range of climax values of $e$ is only $4.74 \leq e \leq 5.50$ for the six catchments studied. It is gratifying and supportive of the climatic climax hypothesis to find in the literature a summary of observations which states [Brutsaert, 1982]'... typical values (of $c$) lie around

<table>
<thead>
<tr>
<th>$n_o$</th>
<th>0.80</th>
<th>1.00</th>
<th>1.10</th>
<th>1.20</th>
<th>1.40</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.20</td>
<td>0.33-30.10</td>
<td>0.20-27.58</td>
<td>0.21-23.10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.25</td>
<td>0.32-18.02</td>
<td>0.25-16.93</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.30</td>
<td>0.30-13.31</td>
<td>0.27-12.86*</td>
<td>0.21-12.20*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.35</td>
<td>0.25-16.93</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.40</td>
<td>0.25-16.93</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.45</td>
<td>0.30-13.31</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Observed $E[Y_A] = 12.50$ cm.

*Single value interpolated between these two.

Observed $E[Y_A] = 58.76$ cm.

**Table 4. Climatic Climax Values of $M_o^* - E[Y_A]$: Neosho River**

**Table 5. Climatic Climax Values of $M_o^* - E[Y_A]$: Chattahoochee River**
four to five. The reasons for this small range can be inferred from the water balance formulation. To begin with, $c$ has a lower limit [Brooks and Corey, 1966] given by

$$c > 3.0 \quad (16)$$

Furthermore, since the climatic climax condition is one of maximum $M_0$, it is one of maximum $E_{RsA}$ and minimum $Y_A$. From Eagleson [1978a-g],

$$E[Y_A] = m_{PA} e^{-G} \xi(\sigma) + m_K(1)S_0^c \quad (17)$$

in which $K(1)$ is the saturated hydraulic conductivity. Minimizing $Y_A$ with respect to $c$ gives

$$\frac{\partial \xi(\sigma)}{\partial c} = \frac{\partial S_0^c}{\partial c} \left[ \xi(\sigma)K(1)/2m - m_K(1)e^{C/m_{PA}} \right] \quad (18)$$

The bracketed term on the right-hand side of (18) is of order unity, while the term $\partial S_0^c/\partial c$ is of the order $10^{-2}$ or less over the practical range of $S_0$ for $c$ in the observed range. We thus conclude that another approximate climax relationship is

$$\frac{\partial \xi(\sigma)}{\partial c} = \frac{\partial S_0^c}{\partial c} \approx 0 \quad (19)$$

which is satisfied (except at $S_0 = 1$) only by $\partial \phi(c) = 0$. From the definition of $\phi$ [Eagleson, this issue, appendix], $\partial \phi/\partial c = 0$ gives approximately

$$(c - 3) \frac{\partial \phi}{\partial c} + \phi = 0 \quad (20)$$

where $\phi(c, S_0)$ is the dimensionless infiltration diffusivity [Eagleson, 1978c, p. 727]. By integrating (20), we have

$$(c - 3) \phi(c, S_0) = f(S_0) \quad (21)$$

in which $f(S_0)$ is an undetermined function.

We evaluate $f(S_0)$ using the climatic climax $c - S_0$ pairs given in Table 6. The results are shown in the upper portion of Figure 11a. Representing $f(S_0)$ by its expected value allows us to write the very useful empirical relation

$$(c - 3) \phi(c, S_0) = 0.75 \quad (22)$$

which is presented in the lower half of Figure 11a. For the common range of $S_0$, the form of this curve restricts $c$ to a relatively narrow range. Equation (22) allows elimination of $c$ from the water balance equation in terms of the state variable $S_0$.

### The Saturated Intrinsic Permeability

Minimizing $Y_A$ with respect to $k(1)$ should lead to a companion relation defining the climax saturated intrinsic permeability, but the mathematics is not so simple. Instead, we use the fact that the evaporation parameter $E$ is maximum under climax conditions. In the same manner as above, we apply

$$\frac{\partial E}{\partial k(1)} = 0 \quad (23)$$

Using the definition of $E$ [Eagleson, this issue, appendix] we find

$$\frac{\partial S_0}{\partial k(1)} = -\frac{s_0}{(c + 5)k(1)} \quad (24)$$

integrating

---

**Table 6. Fitted Climax Parameters**

<table>
<thead>
<tr>
<th>Catchment</th>
<th>$n_e$</th>
<th>$k_e$</th>
<th>$M_0^*$</th>
<th>$c$</th>
<th>$\xi(1)$</th>
<th>$E_{RsA}$ cm</th>
<th>$P_{RsA}$ cm</th>
<th>$R_{RsA}$ cm</th>
<th>$E_{RsA}$ cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neosho*</td>
<td>0.20</td>
<td>0.80</td>
<td>0.33</td>
<td>5.45</td>
<td>110</td>
<td>0.34</td>
<td>0.41</td>
<td>1</td>
<td>30.10</td>
</tr>
<tr>
<td>Neosho</td>
<td>0.45</td>
<td>1.30</td>
<td>0.24</td>
<td>5.45</td>
<td>65.1</td>
<td>0.58</td>
<td>0.38</td>
<td>1</td>
<td>12.53</td>
</tr>
<tr>
<td>Santa Paula</td>
<td>0.30</td>
<td>1.00</td>
<td>0.39</td>
<td>5.15</td>
<td>14.9</td>
<td>0.92</td>
<td>0.55</td>
<td>1</td>
<td>17.34</td>
</tr>
<tr>
<td>James</td>
<td>0.18</td>
<td>1.05</td>
<td>0.48</td>
<td>4.81</td>
<td>25.2</td>
<td>1.85</td>
<td>0.50</td>
<td>1</td>
<td>38.20</td>
</tr>
<tr>
<td>James</td>
<td>0.20</td>
<td>1.00</td>
<td>0.52</td>
<td>5.50</td>
<td>42.4</td>
<td>1.95</td>
<td>0.49</td>
<td>1</td>
<td>36.50</td>
</tr>
<tr>
<td>Chattahoochee</td>
<td>0.20</td>
<td>1.05</td>
<td>0.49</td>
<td>5.15</td>
<td>28.5</td>
<td>2.03</td>
<td>0.54</td>
<td>1</td>
<td>59.66</td>
</tr>
<tr>
<td>Chattahoochee</td>
<td>0.25</td>
<td>1.00</td>
<td>0.60</td>
<td>4.95</td>
<td>18.7</td>
<td>3.05</td>
<td>0.56</td>
<td>1</td>
<td>56.85</td>
</tr>
<tr>
<td>Merrimack</td>
<td>0.35</td>
<td>1.00</td>
<td>0.90</td>
<td>4.75</td>
<td>43.2</td>
<td>28.1</td>
<td>0.75</td>
<td>1</td>
<td>51.30</td>
</tr>
<tr>
<td>Clinton</td>
<td>0.35</td>
<td>1.00</td>
<td>0.91</td>
<td>4.75</td>
<td>5.57</td>
<td>34.6</td>
<td>0.72</td>
<td>1</td>
<td>56.80</td>
</tr>
</tbody>
</table>

*Fitted to estimated $E[R_{RsA}]$. 

---

**Table 7. Comparison of Climax Surface Runoff With USGS Estimate**

<table>
<thead>
<tr>
<th>Catchment</th>
<th>USGS $E[R_{RsA}]$, cm</th>
<th>Climax* $E[R_{RsA}]$, cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neosho</td>
<td>10.31</td>
<td>4.42</td>
</tr>
<tr>
<td>James</td>
<td>17.83</td>
<td>18.20</td>
</tr>
<tr>
<td>Chattahoochee</td>
<td>29.44</td>
<td>26.70</td>
</tr>
<tr>
<td>Merrimack</td>
<td>25.25</td>
<td>27.90</td>
</tr>
</tbody>
</table>

*Fitted to observed $E[Y_A]$. 

---

Fig. 8. Evaluation of surface runoff function.
LEGEND

CLIMATIC CLIMAX PARAMETERS

THEORY (EAGLESON, 1978)

\[ f(s_0) = \begin{cases} 0.058 \frac{s_0^{L}}{s_0} & \text{for } \frac{s_0}{s_0} \\ 0 & \text{for } \frac{s_0}{s_0} \end{cases} \]

Equation (26) allows elimination of \( k(1) \) from the water balance equation in terms of the state variable \( s_0 \).

THE DISTRIBUTION OF ANNUAL YIELD

A further test of the climax properties is gained by using them to calculate the cumulative distribution function (cdf) of annual yield. The average annual water balance is used as a first order approximation to the annual water balance, and the distribution of \( Y_A \) is derived from the known distribution of \( P_A \) [Eagleson, 1978a–g]. We expect the mean annual yield to be correct because we have determined the \( k_0 - n_s \) values by fitting the average observed annual streamflow. Furthermore, in humid climates where the \( P_A - Y_A \) relationship is closely linear, we expect the variance of \( Y_A \) to be predicted well, since it is nearly the same (the known) variance of \( P_A \). In arid climates, however, the \( P_A - Y_A \) relationship is nonlinear and the variances differ. Prediction of the cdfs in the more arid climates will thus be the more severe test of the climax hypothesis. Of course, it is just these dry climates in which the assumed equivalence of annual streamflow and annual yield is most likely to break down.

The cdfs for the six catchments of Table 6 are represented in Figures 12–16 in the order of their increasing aridity as measured by the dimensionless evaporation parameter \( E \). On each figure the observed annual streamflows are shown using the Thomas [1948] plotting position. Predicted cdfs using indicated climax properties are shown as solid lines. The boxed set of properties is that which produces the observed average annual yield.

The Merrimack and Nashua catchments are geographical neighbors and have the same variance of \( P_A \). Interestingly,
the climax properties fitting the observed average yields were identical even though the catchment areas are widely different: 174 km² for Nashua and 11,554 km² for Merrimack. This is only modest evidence of the robustness of the method because (Table 1) only the temperature and mean annual precipitation were taken to differ at the two sites. These facts enable the cdf comparisons for these two catchments to be presented together, as is shown in Figure 12.

The Chattahoochee catchment is shown in Figure 13. Here we found two climax $k_v - n_v$ pairs that approximated the observed average yield. As can be seen from Table 5, these values probably reduce to one, having intermediate $k_v$ and $n_v$ values, if the observed yield is reproduced exactly. The agreement with the observed cdf is again excellent. The extra cdf with unboxed parameter values is for climax properties producing only about 90% of the observed yield. This demonstrates the cdf sensitivity to $n_v$. Two $k_v - n_v$ pairs were also found for the James River catchment (both by interpolation in $k_v$ at constant $n_v$) as is shown in Figure 14. Once again, further interpolation would probably reduce them to a common $k_v - n_v$ pair. Here also the agreement with observation is quite good.

The Santa Paula Creek catchment is presented in Figure 15. The observed cdf for this catchment has a sag which apparently originates in the observed $P_A$ [Eagleson, 1978a-g]. In deriving these cdf’s, we have used a fitted analytical cdf of $P_A$; thus we cannot expect to predict this sag. Nevertheless, once we correct the climax cdf by allowing the vegetation density to vary annually with the precipitation, the agreement is quite good in both tails.
The last of these comparisons, for the Neosho River, is the most interesting and is shown in Figure 16. Here the climax $k_v - n_e$ pair that predicts the average yield far underestimates its variance. No set of climax parameters could be found that reproduced both the mean and the variance of $Y_A$. However, we have an estimate of the average annual surface runoff for this catchment. If we use this as the observation to be fitted in selection of the climax parameters, we obtain the set circled on Figure 16. This set produces an average yield that is 250% of the average observed streamflow. However, it produces a variance of total yield that more nearly approximates the variance of observed streamflow. It may be that infiltrated water does not reenter the stream channels of this catchment and that the observations are more nearly surface runoff than total yield. On the other hand, perhaps the system is suboptimal in that it has not yet reached the climatic climax, or perhaps the empirical algorithm for hydrograph separation breaks down under these conditions.

We can see in Figure 16 how sensitive the variance of $Y_A$ is to soil porosity. The yield becomes larger as $n_e$ gets smaller.

### THE OPTIMUM VEGETATION PARAMETERS

#### Moist Systems

Thus far we have concentrated our tests largely on the climatic climax hypothesis. We have shown that soil and vegetation parameters determined according to this hypothesis do indeed give predicted water balance behavior that is in reasonable accord with observations.

Eagleson [this issue] also suggested that the difference in time scale between the process of vegetation optimization (canopy density and species) and the process of soil development would insure that the vegetation of a climatic climax soil-vegetation system would itself be optimum but that the reverse would not necessarily occur. We will check this now by comparing the $M_0^*$ and $k_v$ values of the largely moist climax systems of Table 6 with the hypothesized optimum vegetation conditions shown graphically in Figure 1. This is done for nominal values of the surface retention and water table parameters. The comparison is made in Figure 17 and the agreement is very good.

To understand the significance of Figure 17, a second illustration will help. In Figure 18 are presented several $M_0 - E$ curves for the $k_v > 1$ condition. It is these curves that govern the vegetation optimization [Eagleson, 1982] when $M_0 > 0.42$. The hypothesis states that, in a given climate, a given species will maximize its biomass productivity by seeking maximum canopy density. The limit of the density is given by the maximum of the particular $k_v$ curve, and it is the locus of these $M_0 - k_v$ maxima which is presented as the optimum curve for large $M_0$ on Figures 1 and 17. We must remember, however, that once we fix the climate and the species water use coefficient ($k_v$), the value of $E$ has a relatively narrow range of possible values. It will vary with the soil and with $M_0$ (through $s_0$). If the soil is also fixed, $M_0$ and $E$ are single valued.
Since the climax canopy density is an $M_0$ (i.e., maximum soil moisture for given soil), all climax conditions will lie on the appropriate $k_0$ curve of Figure 18. Where they appear depends upon the value of the climate-soil parameter $E$. This is illustrated by the plotting on Figure 18 of several climatic climax states for the James and Neosho rivers. The climatically determined value of $E$ is what places these points at 'suboptimal' $M_0$ in Figure 18 and hence on Figure 17 also.

The large $M_0$ curve of Figure 17 is thus only an upper limit to the $M_0$ for a given $k_0$, and if soil changes are not involved in the vegetal optimization (the relative time scale argument again), the climate determines how close to this limit a given system will come. For dry climates (small $E$) and $k_0$ only slightly greater than unity, the separation will be great. For moist climates (large $E$) and $k_0$ much greater than unity, the gap will be smaller. In fact, in the latter case when the $E$ exceeds the value $E_0$ necessary to put the climax value at the maximum possible $M_0$ for the given $k_0$, the $M_0$ falls off. There is, as we see in Figure 18, a maximum $E = E_{\text{max}}$ for each $k_0$, above which the soil moisture cannot be maximized. This fact was noted earlier. In such cases there would probably be ecological pressure toward a smaller $k_0$ by species substitution.

One more feature of Figure 18 deserves mention and a bit more speculation. Consider a climate-soil system ($E$) with a vegetation species ($k_0$) such that $E_0 < E < E_{\text{max}}$. There are now two values of $M_0$ for this $E$ and $k_0$. Could this be evidence of potential intransitivity in humid systems?

In evaluating all of this discussion about Figure 17, it is important to note (see Tables 4 and 5) that a variation of $k_0$ from 1 to 1.1 (for constant $n_e$) causes only a small change in the predicted yield. This change amounts to 11% in the dry Neosho system but only 4% in the moist (and hence insensitive) Chattahoochee catchment. For water balance calculations, therefore, it may be sufficient to represent the vegetation for moist nonequilibrium conditions (i.e., $M_0 > 0.42$) by the simple relation $k_0 = 1$. This accounts for the dashed line on Figure 17.

It will be convenient to have the curves of Figure 17 in analytical form. Using the above approximation for moist systems, we have the fitted relation

$$k_0 = 1 \quad M_0 \geq 0.42$$

$$k_0 = 0.0018 + 2.66 M_0 - 6.73 M_0^2 + 15.10 M_0^3 \quad M_0 < 0.42$$

$$k_0 = -0.0018 + 2.66 M_0 - 6.73 M_0^2 + 15.10 M_0^3 \quad M_0 > 0.42$$

$$(27)$$

$$(28)$$

$$(29)$$

**Dry Systems**

The catchments of Table 2 are largely dry systems and may be used to verify the dry portion of the optimum vegetation relations. Here measurements of $k_0$ are not available nor are the rainstorm parameters that are needed to calculate the climax conditions. Instead we will use the results of Eagleson [this issue] to transform the $k_0 = k_0(M_0)$ functions of Figure 17 into $\beta = \beta(M_0)$ functions. These are shown as the solid lines of Figure 19 in comparison with the dry catchment data of Table 2. The scatter of the data is quite large. Also shown on this figure as a dashed line is the minimum stress canopy density for $k_0 = 1$. This is the same as the uppermost curve of Figure 4 and forms an upper bound to the observations.

The lower dashed curve is an empirical relation developed by Czarnowski [1964]:

$$\beta = M_0 [1.17 M_0 + 0.4 M_0^{1/2}]$$

$$(28)$$

Equation (28) was developed from a study of very many catchments in the semidesert, prairie, and forest regions of the European portion of the U.S.S.R. It is remarkably similar to the solid curve derived here based on the optimum vegetation hypothesis and must be viewed as an extension of the data sample when evaluating this hypothesis.

This result is the weakest of those tests presented here, but the data used are also the most uncertain. In particular we must remember that the actual evapotranspiration was estimated for these dry catchments by subtracting observed streamflow from observed precipitation. In these arid circumstances, the streamflow certainly underestimates the total yield; hence the evapotranspiration and $\beta$ are both overestimated.

Continuing the simplified $k_0 = 1$ representation of the moist system, the optimum vegetation conditions give the fitted relationship

$$\beta = 0.13 - 0.40 M_0 + 4.75 M_0^2 \quad M_0 < 0.42$$

$$\beta = 0.65 + 0.80 M_0 - 0.45 M_0^2 \quad M_0 \geq 0.42$$

Equation (29) should be useful in estimating the elements of the average annual water and heat balances, given the input precipitation and net radiation and an observation of canopy density.

**Applications**

Computation of the climatic climax soil and vegetation properties can be onerous. The following procedures are...
Fig. 19. Test of minimum stress hypothesis for equilibrium plant coefficient.

Proposition

Natural soil-vegetation systems seek a long-term equilibrium state through gradual synergistic development, such that the minimum stress canopy density is maximized. This is verified well in all but the driest of the six catchments tested. The catchments covered an area range of from 60 to 16,000 km$^2$.

These propositions can be used to estimate the equilibrium values of canopy density, plant water use coefficient, saturated intrinsic permeability of soil, and soil pore disconnectedness index, given only the properties of the climate and the effective porosity of the soil. Need for the latter can, of course, be eliminated using observations of canopy density or of total water yield.

Additional tests of these hypotheses are needed, particularly in arid climates. To accomplish this it is necessary to find data sets from natural catchments containing both observations of canopy density and estimates of average annual evapotranspiration, as well as the input climatic variables.

Summary and Conclusions

Hypotheses regarding the ecological optimization of water-limited natural soil-vegetation systems are tested through comparison with limited field observations, and their application to the parameterization of large-scale land surface hydrology is suggested. The hypotheses are:

**Proposition**

Natural vegetation systems seek a short-term equilibrium state (i.e., canopy density and water use coefficient) such that water demand stress is minimized. This is verified well for humid and semiarid catchments. For arid catchments with $M_0 < 0.3$, the verification is poor, but this is believed to be due to the overestimation of evapotranspiration efficiency resulting from equating observed streamflow and water yield.

**NOTATION**

- $A$: catchment area, km$^2$.
- $A_s$: short-wave albedo of surface.
- $B_p$: average rate of biomass production, g cm$^{-2}$ s$^{-1}$.
- $c$: soil pore disconnectedness index.
- $E$: dimensionless exfiltration parameter.
- $E_{PA}$: annual potential evapotranspiration, cm.
- $E_{PS}$: seasonal potential evapotranspiration, cm.
- $E_{PA}$: average annual evapotranspiration, cm.
- $E_{PS}$: seasonal evapotranspiration, cm.
- $e_p$: average potential rate of evaporation from bare soil, cm d$^{-1}$.
- $G$: gravitational infiltration parameter.
- $h_0$: water retention capacity of surface, cm.
- $k(1)$: saturated intrinsic permeability of soil, cm$^2$.
- $k_d$: potential transpiration efficiency of plant species, equal to the plant coefficient.
- $k_{vo}$: equilibrium plant coefficient.
- $L_e$: latent heat of vaporization, cal g$^{-1}$.
- $M$: vegetation canopy density (i.e., shadowed fraction).
- $M_0$: vegetation canopy density at maximum soil moisture.
- $M_{0*}$: climatic climax vegetation canopy density.
- $m_{PA}$: average annual precipitation, cm.
- $m_l$: average rainstorm intensity, cm d$^{-1}$.
- $m_{lb}$: average time between rainstorms, d.
- $m_{tr}$: average rainstorm duration, d.
- $m_e$: average length of rainy season, d.
- $N$: seasonal average fractional cloud cover.
- $n_e$: effective porosity of soil.
- $P_A$: annual precipitation, cm.
- $P_S$: seasonal precipitation, cm.
- $q_b$: average net rate of outgoing long-wave radiation, cal cm$^{-2}$ min$^{-1}$.
- $q_l$: average seasonal rate of insolation at surface, cal cm$^{-2}$ min$^{-1}$.
- $R_{PA}$: annual groundwater runoff, cm.
- $R_A$: annual surface runoff, cm.
- $S$: saturation ratio.
- $s_0$: long-term average soil moisture concentration in root zone.
Acknowledgments. This work was performed with the support of NASA Goddard Space Flight Center under grants NAG 5-89 and NAG 5-134. Stefanos Andreou, research assistant in the Department of Civil Engineering at the Massachusetts Institute of Technology, assisted with the computation.

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(Received July 20, 1981; revised December 18, 1981; accepted December 29, 1981.)