

# Ecological Optimality in Water-Limited Natural Soil-Vegetation Systems

## 1. Theory and Hypothesis

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The solution space of an approximate statistical-dynamic model of the average annual water balance is explored with respect to the hydrologic parameters of both soil and vegetation. Within the accuracy of this model it is shown that water-limited natural vegetation systems are in stable equilibrium with their climatic and pedologic environments when the canopy density and species act to minimize average water demand stress. Theory shows a climatic limit to this equilibrium above which it is hypothesized that ecological pressure is toward maximization of biomass productivity. It is further hypothesized that natural soil-vegetation systems will develop gradually and synergistically, through vegetation-induced changes in soil structure, toward a set of hydraulic soil properties for which the minimum stress canopy density of a given species is maximum in a given climate. Using these hypotheses, only the soil effective porosity need be known to determine the optimum soil and vegetation parameters in a given climate.

### INTRODUCTION

The water and heat balances of a land surface are coupled strongly through the evapotranspiration-latent heat equivalence. Estimation of the evapotranspiration over large areas is therefore a central problem of hydroclimatology.

Evapotranspiration and the other soil moisture fluxes are dependent upon the hydraulic properties of the root zone soil and upon the water use characteristics of the vegetation canopy. Because of the large spatial variability of the properties of natural soils [Nielsen *et al.*, 1973], and because of the high degree of nonlinearity of the fluxes, spatial averaging over the large area elements of either climate or water resource models becomes a nontrivial problem. It must usually be accomplished without adequate information about the properties and states of a soil system which is hidden from ready observation.

The natural vegetal cover can be easily observed, however, and its state (for a given climate) is known to provide an integrated reflection of the subsurface conditions [Walter, 1973]. The time constant of vegetation growth is large with respect to that of the soil-wetting weather system, and the canopy root system encounters the full range of soil variability. We will therefore look to the state of the vegetation canopy for information about the time and space average evapotranspiration.

Furthermore, the recognition by many investigators [e.g., L'vovich, 1979, p. 34] that there may be intermediate values of soil hydraulic properties at which evapotranspiration is a maximum raises the possibility of there being an ecologically optimum joint state of vegetation and soil toward which natural systems evolve in a given climate. Corroboration of such an ecological optimum would permit macroscale parameterization of both soil and vegetation where only climate is known—the best of all possible hydrological worlds.

This paper is devoted to presentation of the theoretical and hypothetical basis of this optimality through detailed examination of an average annual water balance relationship

[Eagleson, 1978a-g]. The relationship is approximate in the sense that it trades off physical fidelity in favor of a simplicity designed to facilitate the development of insight and the estimation of parameters. This engineering approximation is particularly apparent in the model's description of both the water use and the biomass production of the vegetation in terms of only canopy density and a species-dependent water use factor. Subsequent testing of the hypotheses should indicate whether increased biological sophistication is required in order to meet the current objectives.

This study is restricted to systems whose biology is limited by either available water or available energy rather than by nutrients, pests, disease, or predators. Furthermore, it deals only with natural systems that are not cultivated, irrigated, or artificially fertilized. A subsequent paper [Eagleson and Tellers, this issue] presents some confirming observational evidence and discusses applications.

### ECOLOGICAL BACKGROUND

#### *Pedology*

Soil is produced through the interaction of several factors: climate, parent material, vegetation, other biotic agents, and topographic relief [Cruickshank, 1972]. In most cases the first three predominate in an interactive fashion that is illustrated schematically in Figure 1. While climate may not be the dominant factor in all cases, it does influence soil formation in various ways: transportation of the parent material, mechanical and chemical weathering of the parent material, generation of internal soil processes which develop soil features (i.e., pedogenesis), and erosion of the soil body. We are concerned here primarily with pedogenesis.

Different lithological characteristics of the parent rock are important, because [Eyre, 1968] rocks differ greatly in their amount of soluble plant nutrients and because the residue of weathering can vary from 100% clay to 100% quartz. The mix of the latter residuals controls the textural class of the soil (e.g., sandy, silty, clayey) and hence affects not only the hydraulic properties of the soil (e.g., porosity and conductivity) but also the soil chemistry and fertility. Soil development is thus accompanied by vegetation development.

The weathering products can be divided according to their relative solubility in the weak carbonic acids present in most

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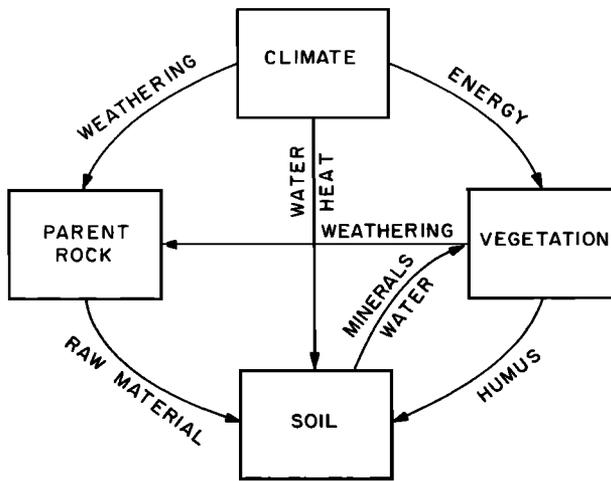


Fig. 1. Soil genesis.

precipitation. Parent rock of predominately basic composition (e.g., basalt and shale) will, in the presence of sufficient water, weather chemically to yield their potassium, magnesium, and calcium to the soil solution as carbonates which contain some of the most important mineral foods required by vegetation [Eyre, 1968]. Furthermore, the poorly soluble constituents of these basic rocks constitute a fine-particled argillaceous (i.e., clayey) residue with a large water-holding capacity (i.e., high porosity and low conductivity). These hydraulic properties limit the penetration of precipitation into the soil but tend to retain the solutes. The clayey soils thus favor shallow-rooted vegetation.

Parent rock of predominately acidic composition will be relatively inert to the precipitation and may weather primarily by mechanical means. Common acidic igneous rocks such as granite contain a large fraction of inert quartz along with some clay-forming feldspar and mica. These silicious rocks weather to produce a largely arenaceous (i.e., sandy) residue which transmits water so readily that the solutes are not retained in the soil matrix. The sandy soils thus support primarily deep-rooted vegetation.

#### Soil Hydraulic Properties

Of course, soils evolve having a continuous spectrum of textures from clay through silt to sand and gravel. The critical hydraulic properties of soil vary widely even within the same textural class, but over the variety of classes their range is enormous. The overall behavior may be generalized, however, as is shown in Figure 2. In this illustration,

- $n$  total porosity, equal to the volume of voids/volume of soil;
- $s_r$  inactive porosity, equal to the void fraction not participating in soil water movement under 'normal' potential gradients;
- $n_e$  effective or active porosity, equal to  $n(1 - s_r)$ ;
- $k(1)$  saturated effective permeability,  $\text{cm}^2$ .

Brooks and Corey [1966] show that  $k(1)$  is related to both the shape (i.e., tortuosity) of the pores and to their total size (i.e., porosity). Davis [1969] states that for a given average geometrical configuration of pore space, such as within a particular textural class, the permeability increases with

increasing porosity according to

$$k(1) = Ae^{Bn} \quad (1)$$

The coefficients  $A$  and  $B$  will vary with textural class as sketched in Figure 2a.

For the fine-particled clayey soils the total particle surface area is enormous. The total pore volume which can be occupied by water that is bound to these surfaces through molecular forces is correspondingly large and the inactive porosity  $n_r$  dominates. With increasing sand content this volume decreases and the effective porosity rises. As the sandy soil becomes gravelly, the falling total porosity takes over from the decreasing surface area and the effective porosity becomes smaller. This is sketched in Figure 2b. We see from this diagram that over the clay to sand textural range encompassing most soil, permeability and effective porosity are directly related. We will now look more closely at the vegetation.

#### The Soil-Vegetation Relation

Borrowing the metaphor of Eyre [1968],

... vegetation is the machine in the soil-making factory. The parent rock provides much of the raw material, the climate lubricates and determines the speed of manufacture, but the vegetation ultimately determines the nature of the finished product.

Referring again to Figure 1, climate influences the nature of vegetation primarily through the hydrothermal environment [Cox *et al.*, 1976; Walter, 1973]. The soil, as we have just seen, performs two primary functions in vegetation growth

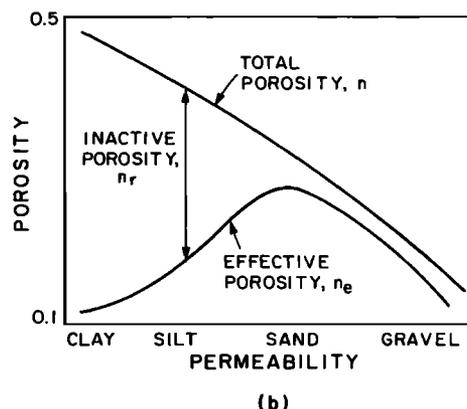
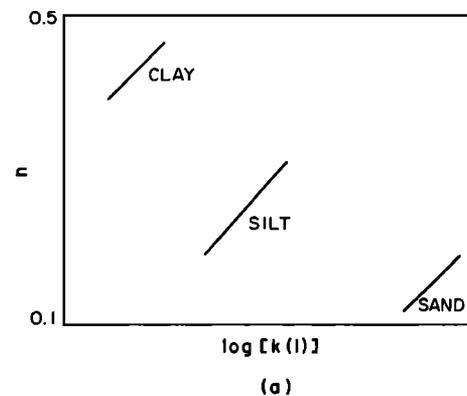


Fig. 2. Variation of soil hydraulic properties with textural class. (a) After Chilingar [1964]. (b) After Bear [1979].

[Eyre, 1968]: providing an inert medium for the storage and conductance of moisture, and providing a chemically active medium for retaining mineral elements in changeable form. These two functions have much to do with the nature of the vegetation which appears in the primary succession.

As plants live and die, they modify the soil by adding organic matter which changes soil texture and thus soil moisture, in addition to providing nutritional elements. Over time, if all else remains constant, the process leads to a 'climax' system which is in stable equilibrium with its surroundings.

According to Eyre [1968], given a favorable climate, forest develops on the sandy porous soils where deep root systems are needed to maintain access to the rapidly percolating rainwater. Leaf fall is worked down into the soil from the surface by this percolation and by the mechanical action of fauna such as worms. This organic matter fills the soil pores, thereby increasing the water-holding capacity and admitting more shallow-rooted vegetal species. In impermeable clays, however, the moisture is concentrated near the surface where it can support primarily the shallow (but densely) rooted species. The continual decay of the roots of these annual species aerates and adds humus throughout the entire root zone, thereby making the soil more permeable and admitting new vegetal species.

#### The Vegetation-Climate Relation

Collinson [1977] describes the relationship between vegetation and climate as 'one of the most difficult problems in ecology.' Indeed, this interaction is at the heart of agricultural science and has occupied researchers since the establishment of agricultural societies. Although whole volumes have been devoted to scientific analysis of the relationship [e.g., Monteith, 1975], a brief description will suffice here.

Vegetation uses solar energy to convert carbon, nitrogen, phosphorous, and other elements into plant tissue. The carbon diffuses through pores in the leaves as carbon dioxide, while the minerals flow in aqueous solution from the soil through the roots. To deal with rates of formation of plant matter requires detailed understanding of species physiology, but to deal with equilibrium conditions, one can learn much from consideration only of plant water use.

Agriculturalists commonly describe plant water use by a species-dependent 'crop coefficient'  $k_c$ , which is the ratio of crop evapotranspiration to the potential evapotranspiration of a reference crop (often short green grass). Total crop water use introduces the canopy density  $M$  (i.e., the shaded fraction of the surface) so that the rate of water use by the vegetated surface fraction is

$$E_v = Mk_c E_{p_0} \quad (2)$$

where  $E_v$  is the rate of actual evapotranspiration from vegetated surface fraction and  $E_{p_0}$  is the potential rate of evapotranspiration from reference crop. The value of  $k_c$  will vary with plant species and with the stage of the seasonal growth cycle [Doorenbos and Pruitt, 1977].

#### WATER-LIMITED EQUILIBRIUM CONDITIONS

##### Soil Moisture

In the short term, conservation of water mass in the root zone gives

$$n_c Z_r \frac{ds}{dt} = i - e_T - p - r_s \quad (3)$$

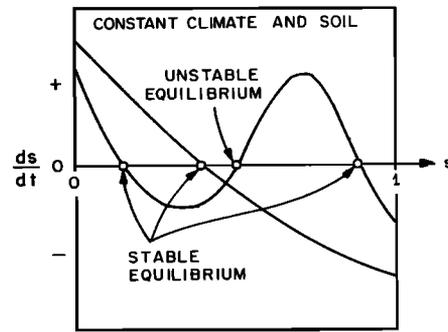


Fig. 3. Equilibrium of soil moisture.

where

- $Z_r$  depth of root zone, cm;
- $s$  concentration of soil moisture;
- $t$  time, s;
- $i$  precipitation intensity,  $\text{cm s}^{-1}$ ;
- $e_T$  rate of evapotranspiration,  $\text{cm s}^{-1}$ ;
- $p$  rate of percolation out of bottom of root zone,  $\text{cm s}^{-1}$ ;
- $r_s$  rate of storage and runoff of surface water,  $\text{cm s}^{-1}$ .

Equilibrium of soil moisture is a fundamental ecological condition determining the moisture climate for plant and soil development. It is given by the mathematical roots of (3):

$$\frac{ds}{dt} = 0 \quad s = s_0 \quad (4)$$

When the soil is dry ( $s = 0$ ), it can only get wetter, and  $ds/dt$  is positive. When the soil is saturated ( $s = 1$ ) it can only get drier, and  $ds/dt$  is negative. Thus, for a given climate and soil, there must be at least one stable root,  $s = s_0$ , for which a small perturbation in  $s$  produces a negative feedback that returns the system to the equilibrium condition. Possible examples of one and two stable equilibria are sketched in Figure 3. We will not worry here about the number of roots or whether a given root is stable or unstable. That is the subject of continuing research. Here we will deal only with the equilibrium condition which, by time-averaging equation (3), is [Eagleson, 1978]:

$$E[P_A] - E[E_{T_A}(s_0; \text{climate, soil, vegetation})] - E[Y_A(s_0; \text{climate, soil})] = 0 \quad (5)$$

in which

- $P_A$  annual precipitation, cm;
- $E_{T_A}$  annual total evapotranspiration, cm;
- $Y_A$  annual total yield, cm;
- $s_0$  long-term average root zone soil moisture concentration;

$E[ ]$  expected value of  $[ ]$ .

In (5) the term 'climate' is used to represent the several parameters defining the long-term average potential rate of bare soil evaporation,  $\bar{e}_p$  (as given for example by the Van Bavel [1966] modification of the Penman [1948] equation) and those defining the statistics of the rainstorms. The term 'soil' is used to represent the independent hydraulic properties of a homogeneous root zone soil. In Eagleson's [1978a-g] model these are the effective porosity  $n_e$ , the saturated intrinsic permeability  $k(1)$ , and the pore disconnectedness

index  $c$ . The last is defined by

$$c \equiv \Delta[\ln(k)]/\Delta[\ln(s_0)] \quad (6)$$

The term 'vegetation' is used in (5) to represent the parameters defining the canopy water use.

Following (2), *Eagleson* [1978a-g] represented the time-averaged evapotranspiration of the vegetated fraction by

$$E_v = Mk_v \bar{e}_p \quad (7)$$

where  $k_v$  is the species-dependent plant coefficient, equal to the unstressed rate of transpiration/potential rate of bare soil evaporation. The coefficient  $k_v$  differs from the standard crop coefficient  $k_c$  due to the use (by the former) of bare soil as a reference evaporating surface and due to its representation of canopies which are in equilibrium (i.e., full growth) and hence are transpiring at their maximum rate. The range of values of  $k_v$  is expected to be about the same as that observed for  $k_c$  [Doorenbos and Pruitt, 1977], namely  $0 < k_v \leq 1.35$ . The complete form of the evapotranspiration and yield functions of (5) are given in the appendix. In a given climate, (5) gives the equilibrium soil moisture  $s_0$  as a function of five parameters of the soil and vegetation:  $n_e$ ,  $k(1)$ ,  $c$ ,  $k_v$ , and  $M$ .

For fixed soil and climate, (5) gives the equilibrium soil moisture as a function  $M(k_v \text{ fixed})$  or of  $k_v (M \text{ fixed})$  as shown in Figures 4 and 5, respectively. The climates of these figures are defined in Table 1 and the clay (CL), clay loam (CL-L), silty loam (SI-L), and sandy loam (SA-L) soils are defined elsewhere [Eagleson, 1978f, p. 753].

Noting the maximization of soil moisture at intermediate canopy density (Figure 4), *Eagleson* [1978a-g] hypothesized

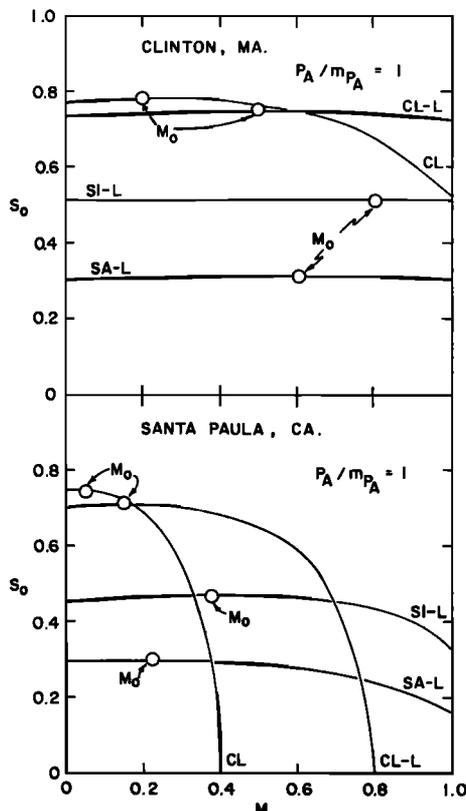


Fig. 4. Solutions of the water balance equation for  $k_v = 1$  [from *Eagleson*, 1978a-g].

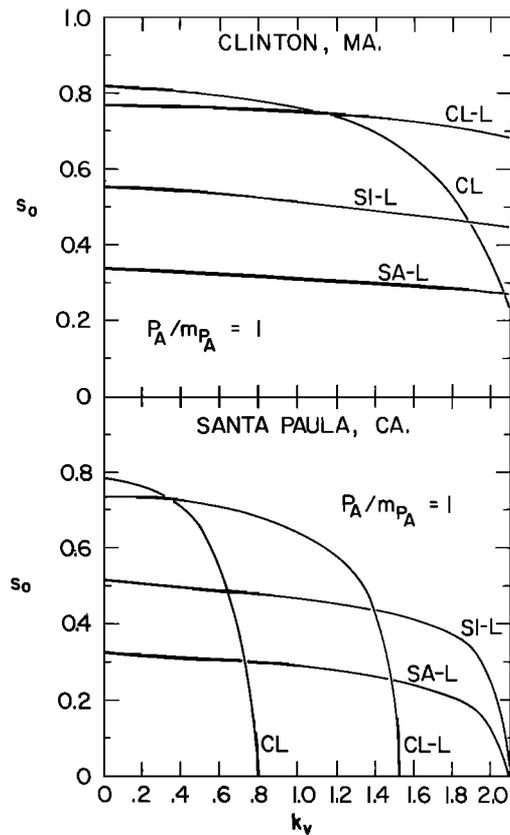


Fig. 5. Solutions of the water balance equation for  $M = 0.5$  [from *Eagleson*, 1978a-g].

that water-limited natural vegetal systems at any seral (i.e., successional) stage will develop a canopy density that produces minimum water demand stress under the local climate and soil conditions. This will tend to maximize the reproductive potential of the plants. A necessary condition for minimum stress is that the soil moisture takes on the maximum value possible. The hypothesis is then that natural vegetal systems tend toward an equilibrium in which soil moisture is maximized. Mathematically this is

$$\frac{\partial s_0}{\partial M} = 0 \quad M = M_0 \quad (8)$$

#### Canopy Density

Of all the vegetation and soil parameters the vegetal biomass is capable of change on the shortest time scale. Perhaps the best example of this is the sudden appearance of annual grasses on a barren arid soil after a rare rainfall. Investigators have long sought to relate the equilibrium biomass to the long-term average evapotranspiration. *Rosenzweig* [1968] reasoned that the actual annual evapotranspiration is an integrated index of the simultaneous availability of the two most important rate-limiting photosynthetic resources: water and solar radiation. It should therefore be a successful predictor of annual vegetation biomass productivity. That is,

$$N_0 = N_0(E_{TA}) \quad (9)$$

where  $N_0$  is the net annual above-ground productivity of plant community in  $\text{g m}^{-2}$ .

TABLE 1. Representative Climate and Soil Parameters

Parameter	Clinton, Mass.	Santa Paula, Calif.
$\bar{e}_p$ , cm d <sup>-1</sup>	0.15	0.27
$m_{i_p}$ , d	3.0	10.4
$m_{t_p}$ , d	0.32	1.4
$m_{r_p}$ , d	365	212
$m_{P_A}$ , cm	111.3	54.4
$\bar{w}$ , cm d <sup>-1</sup>	0	0
$T_a$ , °C	8.4	13.8
$h_0$ , cm	0.1	0.1
$n_e$	0.30	0.30
$k(1)$ , cm <sup>2</sup>	$6.95 \times 10^{-11}$	$1.41 \times 10^{-10}$
$c$	5.05	4.95

Others [e.g., *Whittaker and Niering, 1975*] have related the biomass to leaf area index  $L$ , defined as the total single-sided leaf area per unit of land surface. *Grier and Running [1977]* found a relationship between leaf area index and local water balance.

*Budyko [1974, p. 423]* and *Larcher [1975, pp. 69–70]* proposed that there is an optimum value of  $L$  at which vegetation productivity reaches its maximum with plentiful water. For smaller  $L$  the stand is open, and while each plant gets more light, the biomass per unit of ground area is reduced. For larger  $L$  the stand is increasingly closed, reducing the total absorbed energy to a smaller amount. *Budyko [1974, p. 423]* reasoned that there are probable evolutionary pressures toward this optimum  $L$  wherever soil moisture is not limiting. Observed values of  $L$  range from 2.7 for cotton [*Ritchie and Burnett, 1971*] to 4.5 for deciduous forest [*Walter, 1973*], and 10.2 for spruce forest [*Larcher, 1975*]. *Walter [1973]* confirmed that the light-determined maximum  $L$  for a given species is suppressed by shortages of either water or nutrients.

The leaf area index is often related to the relative intensity of solar radiation by the *Monsi and Saeki [1953]* version of Beer's law of extinction:

$$\frac{I_g}{I_0} = e^{-\mu L} \tag{10}$$

where

- $I_g$  intensity of radiation reaching ground;
- $I_0$  intensity of radiation at top of canopy;
- $\mu$  extinction coefficient (species dependent).

Typical values of  $\mu$  range from 0.35 for grass [*Larcher, 1975*] to 0.40 for many crops [*Ritchie, 1972*] and 0.50–0.77 for trees [*Larcher, 1975*].

Assuming that the ground surface may be disaggregated into a completely shadowed fraction  $M$  for which  $I_g = 0$  and a bare soil fraction  $1 - M$  for which  $I_g = I_0$ , we can use (10) to relate the leaf area index and the canopy density in the species-sensitive form

$$M = 1 - e^{-\mu L} \tag{11}$$

Through (9) and a species-dependent function  $N_0 = N_0(L)$ , this early work establishes that

$$M = M(E_{T_A}) \tag{12}$$

*Rosenzweig [1968]* speculated that where water does limit the biomass production, there may be some optimal efficien-

cy of water utilization that is approached as both short-term succession and long-term evolution proceed. To examine this canopy equilibrium analytically, we will write (5) in the form

$$f_0(s_0, M, k_v; \text{climate, soil}) = 0 \tag{13}$$

We can differentiate (13) to obtain

$$\frac{df_0}{dM} \equiv 0 = \left( \frac{\partial E_{T_A}}{\partial M} \right)_{s_0, k_v} + \left\{ \left( \frac{\partial E_{T_A}}{\partial s_0} \right)_{M, k_v} + \frac{dY_A}{ds_0} \right\} \left( \frac{\partial s_0}{\partial M} \right)_{k_v} + \left( \frac{\partial E_{T_A}}{\partial k_v} \right)_{s_0, M} \left( \frac{\partial k_v}{\partial M} \right)_{s_0} \tag{14}$$

Assuming  $k_v$  and  $M$  are independent and invoking the equilibrium hypothesis of (8), (14) reduces to the equilibrium condition

$$\left( \frac{\partial E_{T_A}}{\partial M} \right)_{s_0, k_v} = 0 \quad M = M_0 \tag{15}$$

Together with (8), (15) gives the additional canopy equilibrium condition

$$\frac{dE_{T_A}}{dM} = 0 \quad M = M_0 \tag{16}$$

which is demonstrated by Figure 6 and comparison with Figure 4. We should note that these equations define a condition of stable equilibrium since, from (8), the pressures of water demand stress on off-peak canopies will always be to restore the minimum stress (i.e., maximum soil moisture) condition.

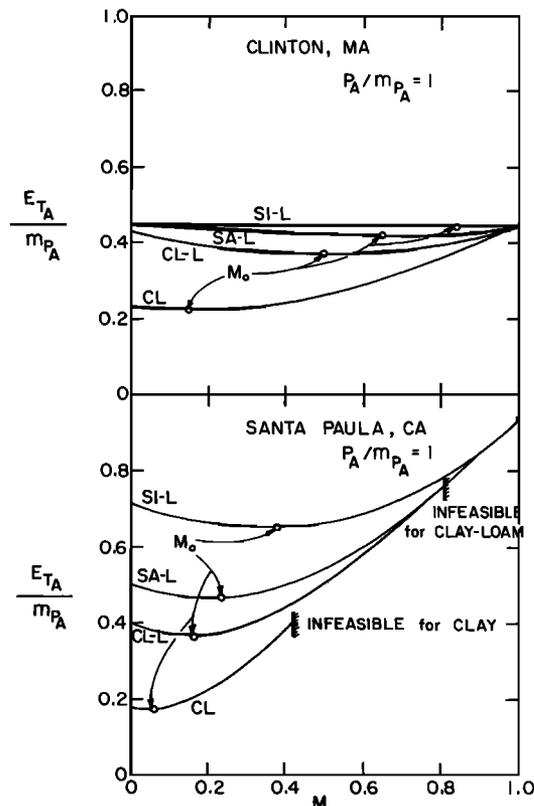


Fig. 6. Minimization of evapotranspiration for  $k_v = 1$  [from *Tellers and Eagleson, 1980*].

Equation (8) or its more convenient equivalent, (15), can be used with (5) to solve for the equilibrium canopy density  $M_0$  of a given species (i.e., fixed  $k_v$ ) for a given climate and soil. This is shown by the solid lines in Figure 7 for the subhumid climate of Clinton, Massachusetts and for the arid climate of Santa Paula, California. At Clinton the system is climate-controlled for the more permeable soils such as the sandy loam (SA-L). In this case the total evapotranspiration is limited by the available energy and solutions are restricted to a narrow range of  $k_v$  around the value unity. Here  $k_v$  can only exceed unity to the extent that the soil properties restrict the bare soil fraction from exfiltrating at the potential rate. As the soils become tighter (i.e., more restrictive of water movement), the range of  $k_v$  increases. At Santa Paula the system is soil-controlled, and the full range of plant coefficients is available. We notice in both cases that as the soils become tighter, the equilibrium canopy of a given species becomes less dense. The dashed lines on Figure 7 represent optimum soil and vegetation conditions which will be discussed later.

We can also use (5) and (15) to derive a theoretical form of (12). It is of practical importance to do so, but first we must review the structure of *Eagleson's* [1978a-g] evapotranspiration function. *Eagleson* used derived distribution techniques to calculate the long-term time averages of the bare soil and vegetal components,  $E[E_s]$  and  $E[E_v]$ , respectively of the total evapotranspiration. Weighting these linearly according to their respective areas gives

$$E[E_{T_A}] = (1 - M) E[E_s] + M E[E_v] \quad (17)$$

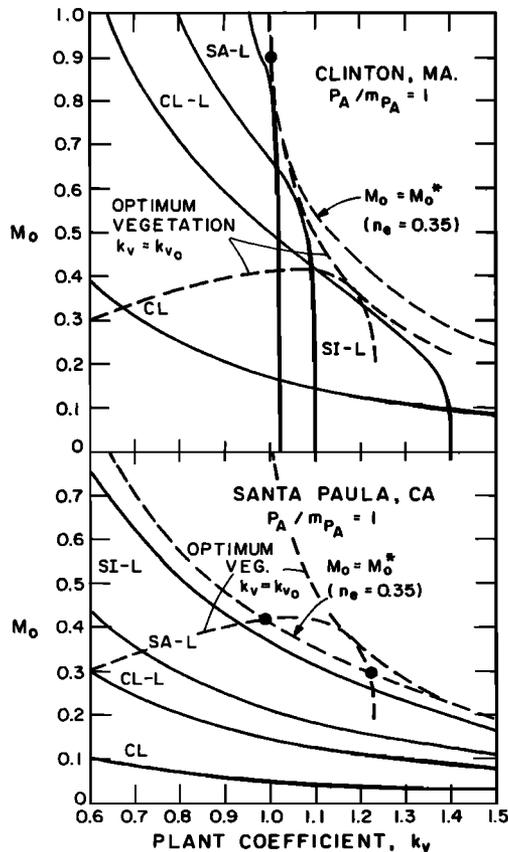


Fig. 7. Equilibrium canopy density in contrasting climates ( $n_e = 0.30$ ).

which can be normalized to obtain

$$\frac{\alpha E[E_{T_A}]}{m_v \bar{e}_p} = (1 - M) \beta_s + M \beta_v \quad (18)$$

where

- $\alpha$  reciprocal of average time between rainstorms,  $d^{-1}$ ;
- $m_v$  average number of interstorm periods per year;
- $\bar{e}_p$  average potential rate of bare soil evaporation,  $cm d^{-1}$ ;
- $\beta_s$  average bare soil evaporation efficiency;
- $\beta_v$  average vegetation transpiration efficiency.

*Eagleson's* hypothesis of minimum water demand stress gives

$$\beta_v \approx k_v \quad (19)$$

and he found that

$$\beta_s = \beta_s(\kappa, \lambda h_0, \alpha h_0 / \bar{e}_p, w / \bar{e}_p, k_v, M, E) \quad (20)$$

where

- $\kappa$  shape parameter of Gamma-distributed rainstorm depths;
- $\lambda$  scale parameter of Gamma-distributed rainstorm depths,  $cm^{-1}$ ;
- $h_0$  surface retention capacity,  $cm$ ;
- $w$  velocity of capillary rise from the water table,  $cm d^{-1}$ ;
- $E$  dimensionless exfiltration parameter (a function of soil moisture, climate and soil parameters, see (A6)).

Equation (20) is given in the appendix to this paper as (A3). Equation (15) can be used to eliminate either  $M = M_0$  or  $E$  from (20).

Recognizing that the weighted mean annual potential evapotranspiration is [*Eagleson*, 1978a-g]

$$E[E_{p_A}] = m_v \bar{e}_p [1 - M(1 - k_v)] / \alpha \quad (21)$$

we can normalize (18) to get the average evapotranspiration efficiency:

$$\beta = \frac{E[E_{T_A}]}{E[E_{p_A}]} = \frac{(1 - M) \beta_s + M k_v}{1 - M + M k_v} \quad (22)$$

where  $\beta$  is the evapotranspiration efficiency and  $E_{p_A}$  is the annual potential bare soil evaporation. This use of the symbol  $\beta$  is in deference to established meteorological convention. Its earlier use by *Eagleson* is given the symbol  $\alpha$  here.

Using (16) and (18), the canopy equilibrium condition becomes

$$\frac{\partial \beta_s}{\partial M} = \frac{\beta_s - k_v}{1 - M} \quad M = M_0 \quad (23)$$

which, together with (A3), allows elimination of  $E$  to write (22) in the form

$$\beta = \beta(M_0; k_v, \kappa, \lambda h_0, \alpha h_0 / \bar{e}_p, w / \bar{e}_p) \quad (24)$$

We will now examine the sensitivity of  $\beta(M_0)$  to its several parameters, as is shown in Figure 8. The parameter  $w / \bar{e}_p$  measures the importance of evaporation directly from the groundwater table. Except in limited areas, the water table will be deep enough so that  $w / \bar{e}_p \ll 1$ . This parameter will be assumed zero throughout this work.

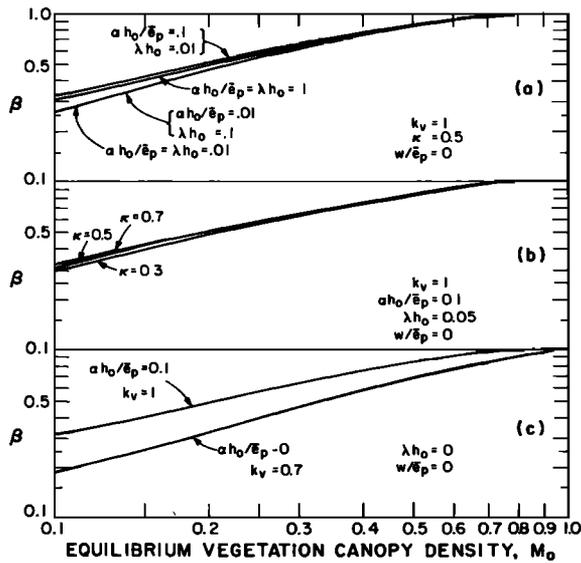


Fig. 8. Sensitivity of the evapotranspiration efficiency [Tellers and Eagleson, 1980].

In Figure 8a,  $k_v$  and  $\kappa$  are fixed at their nominal values of unity and 0.5, respectively, and  $\beta(M_0)$  is presented for the reasonable range of the two surface retention parameters. The parameter  $\lambda h_0$ , which accounts for those small storms that do not satisfy the surface retention capacity, can be seen to be of negligible importance and may be set equal to zero in (A3). The resulting  $\beta_s$  is given in the appendix as (A11). The parameter  $\alpha h_0/\bar{\epsilon}_p$ , which accounts for the effect of surface-retained water in augmenting evaporation, does have a significant effect and must be retained.

In Figure 8b, the effect of  $\kappa$  is examined. This parameter appears in  $\beta_s$  only through the consideration of those storms not satisfying the surface retention capacity. To see its very small effect, parameter  $\lambda h_0$  must retain a nonzero value. For  $\lambda h_0 = 0$ ,  $\kappa$  does not appear in  $\beta_s$ .

In Figure 8c, the dominant effect of  $k_v$  is seen. Because the literature reports values of  $k_v$  which tend to be smaller for plants of the arid zone, the value of the  $\alpha h_0/\bar{\epsilon}_p$  is varied appropriately with  $k_v$ . The two curves shown should bound the majority of observed natural systems. Because  $M_0$  also reflects aridity, it is reasonable to expect observations at high  $M_0$  to follow the  $k_v = 1$  curve and those for small  $M_0$  to be below this curve.

Equations (23) and (A11) can be solved together to find the equilibrium canopy density as a function of the climate-soil parameter  $E$  for constant values of  $k_v$  and the other parameters  $\alpha h_0/\bar{\epsilon}_p$  and  $w/\bar{\epsilon}_p$ . This is presented graphically in Figure 9. It is interesting to note that for  $k_v > 1$ , the canopy density has an upper limit which gets smaller as  $k_v$  gets larger. This limit results from the fact that the sum of the bare soil evaporation and the vegetal transpiration is constrained to be equal to or less than the atmospheric vapor transport capacity  $E_{pA}$ . With the definition

$$H \equiv \alpha h_0/\bar{\epsilon}_p \quad (25)$$

(A11) can be written

$$(1 - \beta_s)e^H = f_1(M, E, k_v, w/\bar{\epsilon}_p) \quad (26)$$

Using (26) and its derivative

$$\frac{\partial f_1}{\partial M} = f_1(M, E, k_v, w/\bar{\epsilon}_p) \quad (27)$$

in (23) gives the equilibrium condition for  $k_v = 1$  (only),

$$f_1(M_0, E, w/\bar{\epsilon}_p) + (M - 1) f_1'(M_0, E, w/\bar{\epsilon}_p) = 0 \quad k_v = 1 \quad (28)$$

which specifies  $E = E(M_0, w/\bar{\epsilon}_p)$  or  $M_0 = M_0(E - w/\bar{\epsilon}_p)$ , independent of  $H$ . These useful functions are approximately by the Chebyshev polynomials

$$M_0 = 0.41 + 0.16 \ln(E) + 9.11 \times 10^{-3} [\ln(E)]^2 - 3.31 \times 10^{-3} [\ln(E)]^3 \quad k_v = 1 \quad (29)$$

$$\ln(E) = -4.56 + 19.58 M_0 - 27.41 M_0^2 + 17.37 M_0^3 \quad k_v = 1$$

**Plant Coefficient**

It is quite possible for the plant species, and hence the water use coefficient  $k_v$ , to change with time. This may occur in the medium term by substitution of one species for another or in the long-term by biological evolution, provided, however, in both cases, that there is pressure for change.

Before attempting an analytical expression of plant coefficient equilibrium, it will be instructive to examine the behavior of (18) and (19) with varying  $M$  and  $k_v$ . This is shown in Figure 10 for the two contrasting climates of Table 1.

Note first that the vegetal component of evaporation is linear in  $M$ , regardless of climate and soil, due to the assumption of unstressed transpiration. The soil component, however, will be linear in  $M$  only when the soil properties do not influence the evaporation rate. This occurs in humid, climate-controlled situations where bare soil evaporation is limited only by the atmospheric vapor transport capacity. As we move to drier climates, the soil component becomes progressively more nonlinear. This is due to the dependence of the exfiltration velocity upon the soil moisture which is in turn influenced by the canopy-dependent extraction of soil moisture by the plant roots. The nonlinearity is a measure of the degree to which the soil component is soil-controlled.

In Figure 10 we see that in the scale of this plot the Clinton system is climate-controlled. In such a case with  $k_v = 1$ , both components behave identically and the total evapotranspiration is a horizontal line, independent of  $M$ . Actually, there is

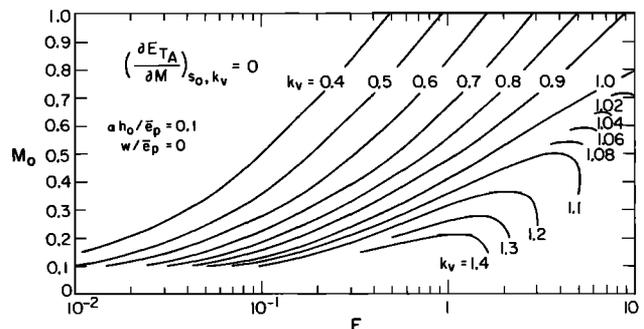


Fig. 9. Generalized equilibrium canopy density.

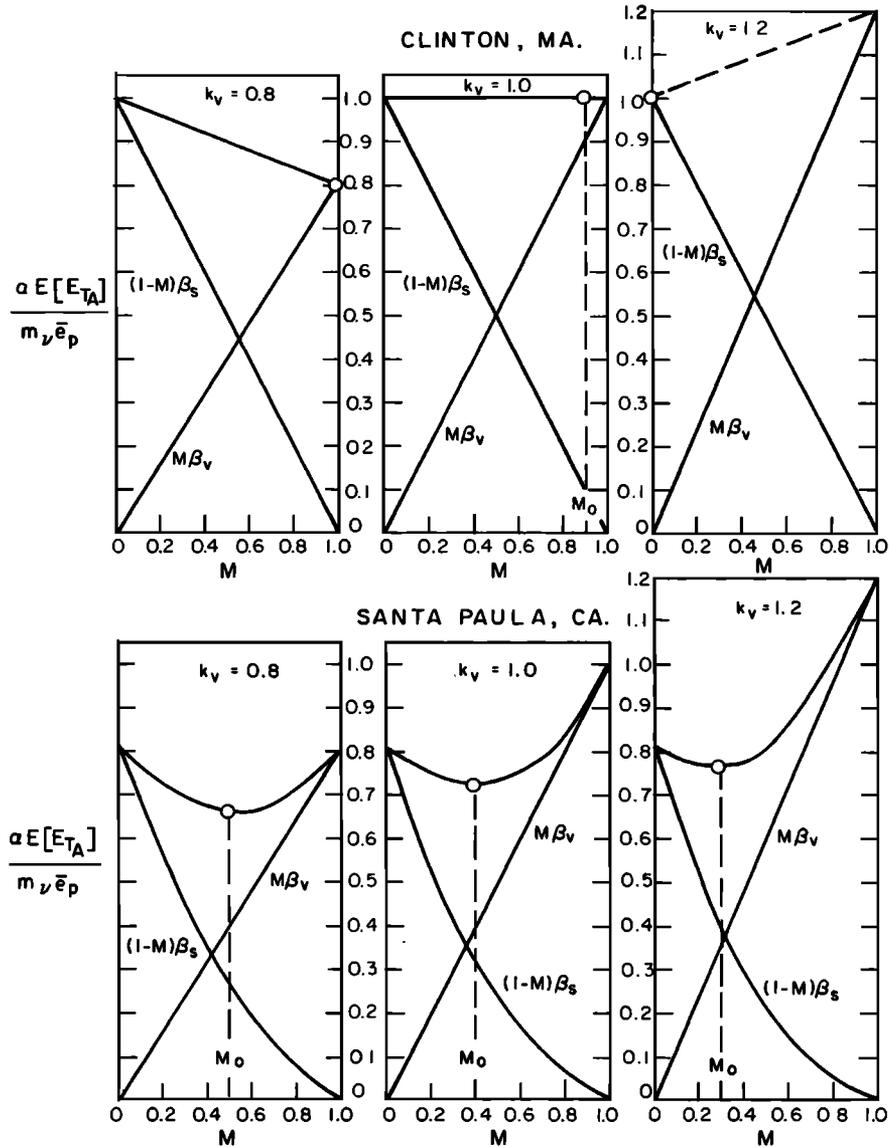


Fig. 10. Decomposition of the total evapotranspiration in contrasting climates ( $\beta_v = k_v$ ).

a slight effect of the soil properties at Clinton leading to a small dip in the total evaporation. The location of the calculated minimum evapotranspiration is indicated by the plotted circle labelled  $M_0$ . In this humid case, we see that  $k_v > 1$  leads immediately to a minimum evapotranspiration at  $M = M_0 = 0$ . This is clearly unrealistic in the humid climate, and we must conclude that there,  $k_v \leq 1$ . For  $k_v < 1$  in the humid case,  $M_0$  will always be unity. As pointed out by *Eagleson* [1978a-g], the rate of canopy water use  $M_0 k_v \bar{e}_p$  is a measure of the rate of production of biomass, which some ecologists believe tends to be maximized in natural systems [Odum, 1971, p. 252]. We might expect, therefore, that  $k_v \approx 1$  in humid systems.

For soil-controlled systems such as Santa Paula, California in Figure 10, the nonlinearity of the soil component produces a clear minimum in total evapotranspiration for all  $k_v$ . In this case, maximization of  $M_0 k_v \bar{e}_p$  leads to  $M_0 = 1$  (at  $k_v < 1$ ) which is in conflict with observations in arid climates. Some other principle must control the selection of  $k_v$  in such systems.

Returning now to the equilibrium condition, we will consider first the long term, where the species change is evolutionary. It seems reasonable to expect in this time scale that survival of recurrent drought will evolve plant species with a  $k_v$  which also maximizes soil moisture. For equilibrium of the plant coefficient therefore, we hypothesize that

$$\left( \frac{\partial s_0}{\partial k_v} \right)_M = 0 \quad k_v = k_{v_0} \quad (30)$$

which, assuming  $M$  and  $k_v$  are independent, implies (by analogy with (14))

$$\left( \frac{\partial E_{TA}}{\partial k_v} \right)_{s_0, M} = 0 \quad k_v = k_{v_0} \quad (31)$$

and also

$$\frac{dE_{TA}}{dk_v} = 0 \quad k_v = k_{v_0} \quad (32)$$

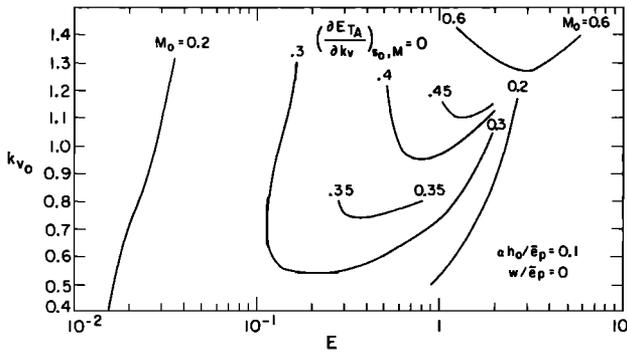


Fig. 11. Generalized equilibrium plant coefficient.

We see from Figure 5, however, that there are at least some conditions under which (30) (and hence its companions, (31) and (32)) cannot be satisfied. We can demonstrate the locus of equilibrium plant coefficients as a function of climate by joint solution of (18), (31), and (A11). This is shown in Figure 11 where  $k_{v_0}$  is given as a function of  $E$  for a few discrete  $M_0$  and for representative values of the parameters  $ah_0/\bar{\epsilon}_p$ . Figure 11 shows clearly that there are regions in which equilibrium, by this criterion at least, is impossible.

In the long term it is reasonable to expect that vegetal equilibrium will be attained with respect to both  $M$  and  $k_v$ . In this case, (15) and (31) must be satisfied simultaneously. Graphically, it means finding those  $M - k_v$  pairs which satisfy both Figure 9 and Figure 11 at the same value of the climate-soil parameter  $E$ . The locus of joint  $M_0 - k_{v_0}$  equilibrium is shown in Figure 12. It is interesting to note that there is a maximum  $M_0 \approx 0.42$  beyond which equilibrium cannot be achieved with respect to both  $M$  and  $k_v$ .

The variation of these paired values of  $M_0$  and  $k_{v_0}$  with climate-soil is shown by their separate dependence on the (common) parameter  $E$  in Figure 13. Notice in this illustration that as the climate-soil system gets more moist (i.e., large  $E$ ), the long-term equilibrium  $k_{v_0}$  increases continuously. The canopy density  $M_0$  increases until  $E \approx 1.4$ , beyond which  $M_0$  falls off with increasing rapidity. There is an apparent maximum  $E \approx 2.8$  at which  $M_0$  goes to zero and beyond which no joint equilibrium of  $M$  and  $k_v$  is possible. This limit is caused by the system coming under climate control, which puts a limit on the total evapotranspiration. Since the soil moisture increases with increasing  $E$  in a given climate-soil system (see (A6)), the bare soil component of evapotranspiration will increase with  $E$  as will the (normalized) vegetation component  $M_0 k_{v_0}$ . The latter is shown as the dashed line in Figure 13. The increasing  $k_{v_0}$  and the climatic ceiling on  $M_0 k_{v_0}$  forces the abrupt decline in  $M_0$  and in  $M_0 k_{v_0}$  predicted by this hypothesis.

While the predicted maximum equilibrium  $k_{v_0}$  ( $k_{v_0} \approx 1.23$ ) is in fair agreement with the maximum  $k_c$  ( $k_c \approx 1.35$ ) reported by Doorenbos and Pruitt [1977], the vanishing of vegetation canopy for  $E > 2.8$  is contrary to all experience. Thus while maximization of soil moisture seems a logical basis for vegetal equilibrium, it appears applicable, if at all, only to dry (i.e., soil-controlled) climate-soil systems.

As the system becomes wetter, the sensitivity of soil moisture to the canopy properties is gradually lost. In Figure 4 we see that the ecological pressures of water demand stress on off-peak  $M$  are not strong due to flatness of the curves

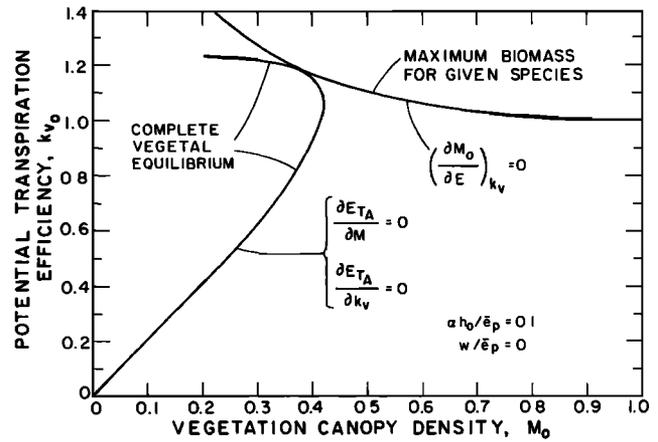


Fig. 12. Optimum vegetation characteristics.

both in Clinton ( $E \approx 34$ ) and in Santa Paula ( $E \approx 2$ ). In Figure 5 we see that for  $M_0 = 0.5$  there is no  $k_v$  in either climate for which (30) is satisfied. This is in agreement with the earlier finding of Figure 12 that complete vegetal equilibrium cannot be obtained for  $M_0 > 0.42$ . By adding the optimum  $k_{v_0} - M_0$  curves of Figure 12 to Figure 7 (as dashed lines), we can see what soils will support equilibrium combinations of  $k_v$  and  $M_0$  in the Clinton and Santa Paula climates.

In only moderately moist systems, therefore, the opportunity for minimum stress equilibrium vegetal systems is lost, and we must find a new ecological equilibrium criterion. To accommodate observed canopy densities which reach unity in wet systems, we must abandon satisfaction of (30), although (8) may still be satisfied.

In the moist system, control shifts from the available water to the available energy. If vegetal systems tend to maximize their reproductive potential and by virtue of plentiful moisture are not subjected to significant water-demand stress, it seems reasonable to expect them to maximize their rate of seed production. As a first approximation to this we hypothesize that the moist system will be under ecological pressure to maximize biomass productivity for the given rate of energy supply. We assume the rate of production of biomass to be proportional to the rate of canopy water use as given by (7). In a given climate and with the plant species fixed through some limitation other than water, maximization of biomass productivity reduces to maximization of canopy density.

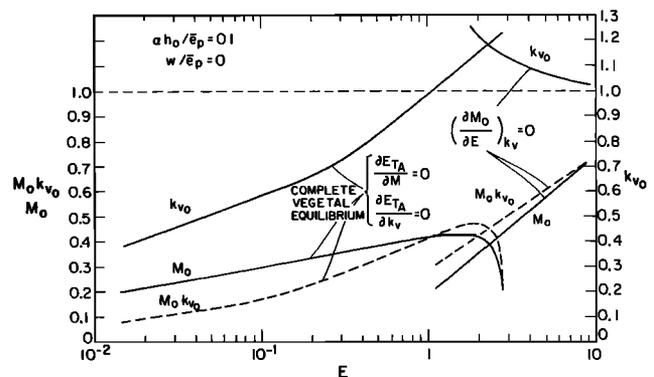


Fig. 13. Variation of optimum vegetation with climate-soil.

We thus assume maximization of reproductive potential in the moist system by operating on the locus of maximum  $M_0$  in Figure 9. Mathematically, the criterion is

$$\left(\frac{\partial M_0}{\partial E}\right)_{k_v} = 0 \quad k_v = k_{v_0} \quad (33)$$

which is the hypothesized optimality condition for moist systems. It is shown as the upper curve of Figure 12 and as the large  $E$  branch of all three curves on Figure 13. To the extent that our measure of biomass productivity  $M_0 k_v \bar{e}_p$  also measures seed productivity, there is continuing ecological pressure to move toward higher  $M_0$  along this curve through the process of species substitution. Under such circumstances, (33) is not an equilibrium condition at the time scale of species substitution. For future reference we have reproduced the optimum vegetation curves of Figure 12 as dashed curves on Figure 7.

*Evapotranspiration Efficiency*

With the equilibrium criteria hypothesized above, we can write the evapotranspiration efficiency  $\beta$  independently of  $k_v$ . This is done using (A11) in which  $k_v$  has been replaced by the locus of solutions to (15) and (31) up to  $M_0 = 0.42$  and with (33) for  $M_0 > 0.42$ . The result is presented as Figure 14 and offers a rational means of estimating average evapotranspiration from large areas without knowledge of soil or vegetation type. Through the hypotheses presented, the equilibrium canopy density is a surrogate for these other parameters.

*Soil Properties*

In discussing the population dynamics of plant communities, *Walter* [1973] notes the existence of ecological optima, that is, environmental conditions under which a species occurs most abundantly in nature. Under the idealized conditions of the laboratory where competition among species can be prevented, the optimum is referred to as a 'physiological optimum' and is shown qualitatively in Figure 15. He notes that the complicating factors of competition cause the ecological and physiological optima to occur

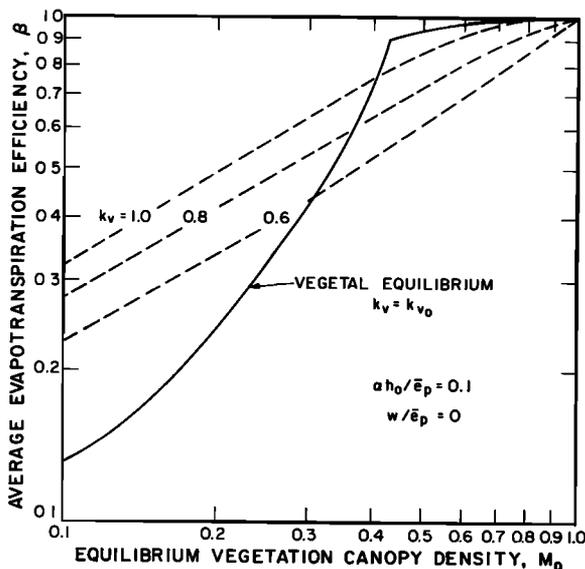


Fig. 14. Average evapotranspiration efficiency.

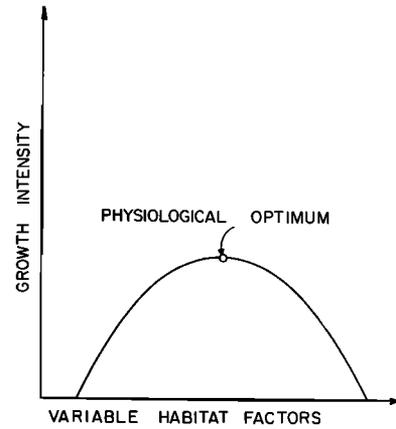


Fig. 15. Idealized ecological optimum [after *Walter*, 1973].

usually at somewhat different points in the plane of Figure 15.

For constant climatic conditions, *L'vovich* [1979, p. 34] sketches the variation of the elements of the mean annual water balance with changing hydrologic characteristics of the soil. The most common form of this variation is reproduced here in Figure 16. *L'vovich* expresses the water balance variation in terms of two hydrophysical characteristics of the soil, the 'infiltration capacity' and the 'water retention capacity.' It usually follows that soils which readily admit water do not retain it well; thus the opposite variation of the two labels on the abscissa of Figure 16.

When the soil has a low infiltration capacity, most of the precipitation becomes surface runoff with only a small amount appearing as groundwater runoff. As soil infiltration capacity increases, a larger fraction of the precipitation enters the soil and thus surface runoff declines. The soil now conducts the infiltration more readily, however, so the groundwater runoff increases. These trends combine to produce a minimum total water yield at an intermediate infiltration capacity. Precipitation is the sum of evapotranspiration and yield, which means that evapotranspiration will be maximum for this intermediate soil. What are the implications of this behavior with respect to vegetation?

We have seen in Figure 14 that evapotranspiration and canopy density are directly related. It is expected then that the gradual long-term textural changes induced in soil by the growth and decay of the vegetation it supports will cause the short-term equilibrium canopy density  $M_0$  to change through a gradual succession of equilibrium states. Following the above, we expect to find a soil of intermediate characteristics for which the equilibrium canopy density is a maximum,  $M_0^*$ . The condition is a physiological optimum in the sense discussed by *Walter* [1973] and sketched here in Figures 15 and 16. For a given vegetal species,  $k_v$  will be a constant, and this optimum state also represents that at which the rate of vegetal water use  $M_0 k_v \bar{e}_p$  is maximum. Again applying the hypothesis that for a given energy supply, biological systems evolve toward a condition of maximum biomass productivity, we expect [*Eagleson*, 1980] that vegetation canopies under constant climatic conditions will develop in synergistic partnership with the soil toward this optimum soil-vegetation state. The negative feedback associated with the maximum makes this a stable equilibrium, provided, of course, that canopy changes do not cause irreversible chemical changes in the soil structure.

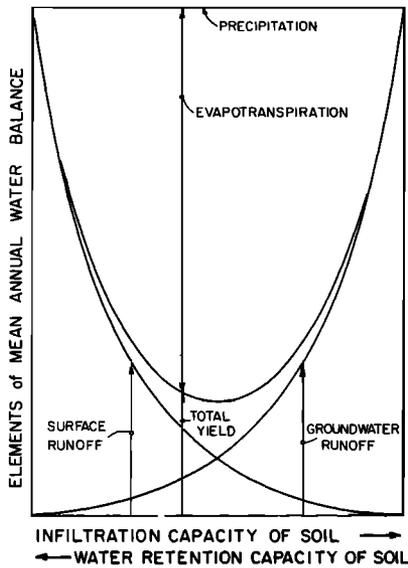


Fig. 16. Variation of water balance with soil characteristics [after L'vovich, 1974].

We will look for this behavior in the water balance by exploring the sensitivity of the water balance elements to variations in the two dynamic soil parameters  $k(1)$  and  $c$ . The third independent parameter  $n_e$  will be kept constant, as will the plant coefficient  $k_v$  and the climate. We will look again at the two contrasting climates, Clinton, Massachusetts and Santa Paula, California (see Table 1). The results are presented in Figure 17. For each pair of  $k(1)$  and  $c$  values, (A1) and (15) are solved to give the equilibrium canopy density  $M_0$ , the average root zone soil moisture concentration  $s_0$ , and the normalized average water balance components, using assumed values of  $n_e$  and  $k_v$ . (Note that the expected value notation has been omitted from these components for convenience.)

The soil moisture and water balance components look similar to those presented earlier [Eagleson, 1978f, p. 752] for the same climates but with bare soil. An exception is the evapotranspiration component where the presence of vegetation produces a peak value in both climates. This peak in evapotranspiration is reflected in a similar peak in the canopy density, as is expected from their direct proportionality as seen in Figure 13. It is this peak canopy density which is of primary interest in this section, and it will be referred to as the 'climatic climax' density,  $M_0^*$ .

The magnitude of  $M_0^*$  and its location in  $k(1) - c$  soil space can be determined most easily from an  $M_0$  contour map, as is sketched in Figure 18. From earlier results with climate  $k_v$ , and  $n_e$  fixed, a line of constant  $M_0$  contains constant values of three other quantities:  $E$  (A2),  $E_{T_A}$  (Figure 14), and  $Y_A$  (A1). Constant  $M_0$  does not mean constant  $s_0$ , however, since the soil properties may vary. At  $M_0 = M_0^*$ ,  $E$ , and  $E_{T_A}$  are also maximum, and  $Y_A$  is minimum.

The long-term equilibrium conditions defining climatic climax soil-vegetation systems are

$$\left(\frac{\partial M_0}{\partial c}\right)_{k(1)} = 0 \quad M_0 = M_0^* \quad (34)$$

and

$$\left(\frac{\partial M_0}{\partial k(1)}\right)_c = 0 \quad M_0 = M_0^* \quad (35)$$

Solution of (34) and (35), along with (15), (A1), and (31), serves to define  $s_0$ ,  $M_0^*$ ,  $k_v$ ,  $k(1)$ , and  $c$  of the equilibrium system in terms of the climate and of the effective soil porosity. The latter parameter is reflective of the parent soil material, and if that is known, or if the conditions of soil formation are known, a reasonable a priori estimate of  $n_e$  can be made.

The soil-space contours of canopy density are presented in Figures 19 and 20 for the climates of Clinton, Massachusetts and Santa Paula, California, respectively. Added to these diagrams are dashed contours of soil moisture concentration to emphasize the fact that this climatic climax hypothesis for soil-vegetation development does not give the global optimum soil moisture. This has arisen because of our assumption that the disparate time scales of canopy density adjustment (short term), of species substitution (medium term), and of soil development (long term) will cause the shorter time scale equilibrium conditions to be satisfied in the longer term. Thus in the longer term the system changes gradually from one  $M_0$  to another  $M_0$ , always locally optimized with respect to soil moisture. The survival pressure to minimize stress by increasing soil moisture is therefore weak. It may guide the direction of the developmental path toward higher biomass, but (we hypothesize) the dominant survival pressure will come from maximization of the reproductive potential through biomass and hence through water use.

It is important to note that satisfaction of (34) and (35) does not mathematically insure satisfaction of either the arid climate vegetal equilibrium, (15) and (31), or the humid climate vegetal optimum (33). We can see this readily for the latter case when we use the chain rule to write

$$\left(\frac{\partial M_0}{\partial E}\right)_{k_v} = \frac{(\partial M_0 / \partial c)_{k(1)}}{dE/dc} \quad (36)$$

By (34) the numerator of (36) is zero for the climatic climax condition. Since  $E$  is also a maximum at  $M_0 = M_0^*$ , the denominator of (36) is also zero. The left-hand side of (36) is thus indeterminate instead of being zero as is required by the vegetal optimum condition (33). For a given  $k_v > 1$ , the value of  $M_0^*$  as given by (34) and (35) cannot exceed the peak  $M_0$  given by (33). As we increase  $M_0$  from zero to find the climax value  $M_0^*$  at some  $k_v$ , we will therefore be operating with an  $E$  that is less than or equal to the value  $E_0$  at which (33) is satisfied. When  $E = E_0$ , our  $M_0$  topography has reached its highest possible elevation for this  $k_v$ , but the contour  $M_0 = M_0^*$  may enclose a finite area in soil space. This  $E = E_0$  ( $M_0 = M_0^*$ ) contour is actually the rim of a volcano. As will be seen in the second paper of this set [Eagleson and Tellers, this issue], contours of ever smaller diameter will show decreasing  $M_0$  but increasing  $E$  until a maximum  $E$  is reached above which the soil moisture can no longer be maximized (for this  $k_v$ ) and the 'crater' becomes bottomless.

To remove this indeterminacy we further hypothesize that the short-term optimum is always satisfied in the long term. This forces  $M_0^*$  to satisfy (33) but reduces the crater to a point in soil space. This hypothesis is evaluated in the second paper of this set [Eagleson and Tellers, this issue].

We must remember that Figures 19 and 20 represent the climatic climax situation in which the constant  $k_v$  is the value that has been reached in the evolutionary process and corresponds to the value  $M_0 = M_0^*$  in accordance with Figure 12. If Figures 19 and 20 were to represent the

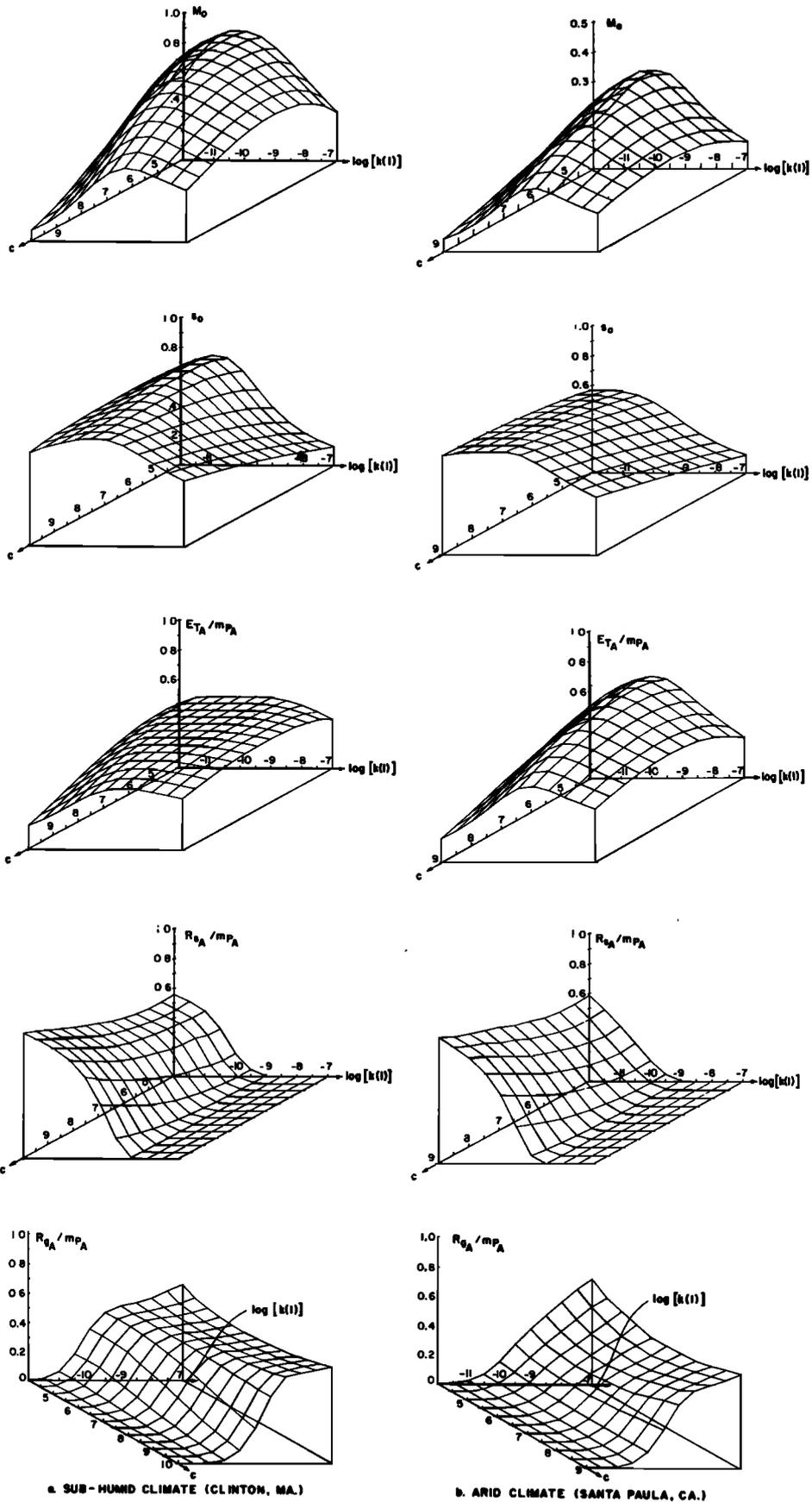


Fig. 17. Sensitivity of water balance to soil parameters for  $k_v = 1$ ,  $n_e = 0.35$  ( $M = M_0$  at each soil pair).

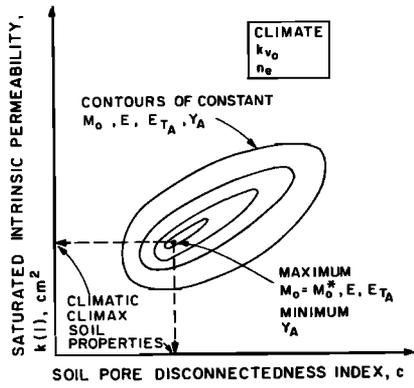


Fig. 18. Climatic climax soil-vegetation system.

developmental history, then each  $M_0$  contour would have to be located using the appropriate but different  $k_v$ , according to Figure 12.

If we repeat Figures 19 and 20 for a range of values of  $k_v$ , we can find the climatic climax canopy density  $M_0 = M_0^*$  as a function of  $k_v$ . This has been done using  $n_e = 0.35$  and is presented as the dashed curves of Figure 7 labeled  $M_0 = M_0^*$ .

In the earlier discussion of Figure 7 we saw that the climate control of humid climate-soil systems truncated the range of feasible  $k_v$ . This truncation is the same phenomenon that causes the crater of  $M_0^*$  in soil space. The edge of this crater is defined by the dashed curve  $k_v = k_{v0}$  on the upper (Clinton) portion of Figure 7 and is touched by the 'corners' of many soil curves at their truncation values of  $k_v$ . This means that in the humid climate each  $M_0 - k_v$  combination requires a different soil. In Clinton only one of these combinations produces the optimum canopy as defined by Figure 12. This is given by the intersection of the  $M_0 - k_v$  and the  $M_0^* - k_v$  curves on Figure 7 and is indicated there by a black dot.

In the arid system as represented by Santa Paula in Figure 7, there is no climate limit to the range of  $k_v$ . Here the  $M_0 - k_v$  and  $M_0^* - k_v$  curves intersect twice, giving two stable climax conditions indicated by the black dots. Because the arid  $M_0^* - k_v$  curve has the same shape as the  $M_0 - k_v$  curves for a given soil, these two climax conditions appear to occur for the same soil. Could this be a cause of intransitivity in arid systems? A similar potential intransitivity can be seen

for humid systems in Figure 9, where for a given  $k_v > 1$ ,  $E$  may be large enough to produce alternate values of  $M_0$ .

SUMMARY AND CONCLUSIONS

The literature concerning ecological optimality of natural soil-vegetation systems has been reviewed and used as a guide to formulate hypotheses governing the equilibrium of water-limited systems with respect to canopy density, species water use, and hydraulic properties of the soil. The statistical-dynamic water balance of Eagleson [1978a-g] is used to quantify these hypotheses. Minimization of water-demand stress is shown to provide a short-term equilibrium condition defining both canopy density and the species-dependent plant water use coefficient for arid climates.

In moist climate-soil systems the soil moisture becomes insensitive to vegetation changes and can be maximized only with respect to canopy density. Maximization of minimum stress canopy density (and hence biomass productivity) for a given plant species provides a rational criterion leading to complete vegetal cover and a plant coefficient of unity for very humid systems. Here the species may be subject to ecological pressure for longer-term change toward higher biomass productivity.

These hypotheses result in a relationship specifying the time average evapotranspiration efficiency of landsurfaces given only the density of the (natural) vegetation canopy, a water table parameter (which is usually zero), and a surface retention parameter. This relationship is independent of the soil properties and hence should be useful, if valid, in estimating the elements of both the water and heat balances given only the properties of the climate.

There is shown to be a set of hydraulic soil properties (saturated permeability and pore disconnectedness index) for which the minimum stress canopy density of a given species has a maximum value in a given climate. Maximization of biomass productivity is then assumed to control the long-term joint development of soil and vegetation.

Combination of these long-term and short-term optimalities specifies the climatic climax vegetation canopy density and the species water use coefficient, as well as two hydraulic properties of the soil and the average soil moisture concentration given only the climate characteristics and the effective porosity of the soil. The analysis reveals potential intransitivities in both arid and humid systems.

Again, contingent upon subsequent verification of these

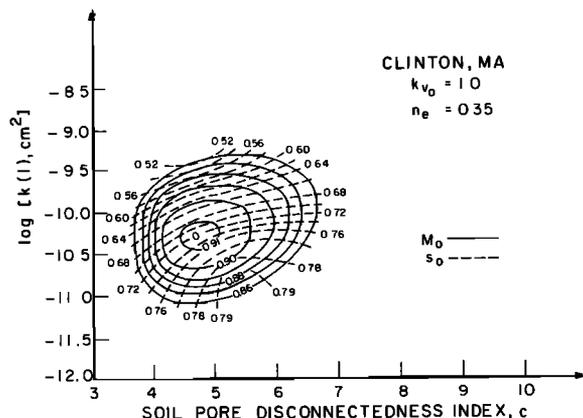


Fig. 19. Climatic climax soil-vegetation system: Clinton, Massachusetts.

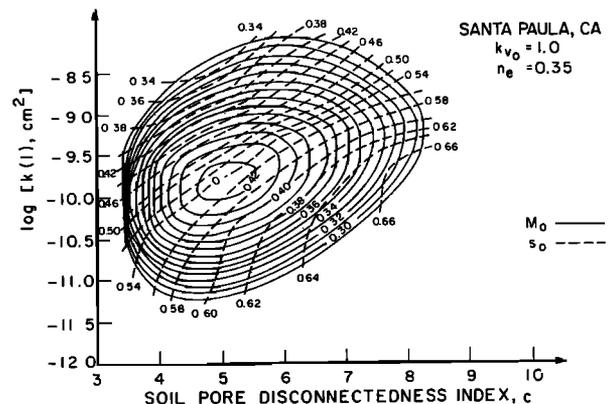


Fig. 20. Climatic climax soil-vegetation system: Santa Paula, California.

relations [Eagleson and Tellers, this issue], it appears possible to make rational estimates of soil and vegetation properties from a minimum of prior information, a capability which should be of great use to hydrologists and hydroclimatologists. Furthermore, these relations should help in the design of stable soil-vegetation systems for use in land reclamation.

#### APPENDIX: THE WATER BALANCE EQUATION

The average annual water balance is given by [Eagleson, 1978a-g]

$$m_{PA} = E[E_{TA}] + E[Y_A] \quad (A1)$$

where

$m_{PA}$  mean annual seasonal precipitation;  
 $E[E_{TA}]$  mean annual total evapotranspiration;  
 $E[Y_A]$  mean annual water yield (i.e., surface plus groundwater runoff).

The evapotranspiration component is

$$\frac{\alpha E[E_{TA}]}{m_v \bar{e}_p} = (1 - M) \beta_s + M k_v \quad (A2)$$

where

$\alpha$  reciprocal of average time between rainstorms,  $d^{-1}$ ;  
 $m_v$  average number of rainstorms per year;  
 $\bar{e}_p$  average potential rate of evaporation from bare soil,  $cm d^{-1}$ ;  
 $\beta_s$  average bare soil evaporation efficiency;  
 $M$  vegetation canopy density, equal to the shadowed fraction of surface;  
 $k_v$  species-dependent plant coefficient, equal to the unstressed rate of transpiration/potential rate of bare soil evaporation.

The bare soil evaporation efficiency  $\beta_s$  is given by

$$\begin{aligned} \beta_s = & \frac{\gamma[\kappa, \lambda h_0]}{\Gamma(\kappa)} - \left[ 1 + \frac{\alpha h_0 / \bar{e}_p}{\lambda h_0} \right]^{-\kappa} \frac{\gamma[\kappa, \lambda h_0 + \alpha h_0 / \bar{e}_p]}{\Gamma(\kappa)} e^{-BE} \\ & + \left\{ 1 - \frac{\gamma[\kappa, \lambda h_0]}{\Gamma(\kappa)} \right\} \left\{ 1 - e^{-BE - \alpha h_0 / \bar{e}_p} [1 + M k_v] \right. \\ & + (2B)^{1/2} E - w / \bar{e}_p + e^{-CE - \alpha h_0 / \bar{e}_p} [M k_v + (2C)^{1/2} E - w / \bar{e}_p] \\ & \left. + (2E)^{1/2} e^{-\alpha h_0 / \bar{e}_p} \left[ \left( \frac{3}{2}, CE \right) - \left( \frac{3}{2}, BE \right) \right] \right\} \\ & + \left[ 1 + \frac{\alpha h_0 / \bar{e}_p}{\lambda h_0} \right]^{-\kappa} \frac{\gamma[\kappa, \lambda h_0 + \alpha h_0 / \bar{e}_p]}{\Gamma(\kappa)} \left\{ (2E)^{1/2} \left[ \gamma\left(\frac{3}{2}, CE\right) \right. \right. \\ & \left. \left. - \gamma\left(\frac{3}{2}, BE\right) \right] + e^{-CE} [M k_v + (2C)^{1/2} E - w / \bar{e}_p] \right. \\ & \left. - e^{-BE} [M k_v + (2B)^{1/2} E - w / \bar{e}_p] \right\} \quad (A3) \end{aligned}$$

where

$\kappa$  shape parameter of Gamma distribution of rainstorm depths;  
 $\lambda$  scale parameter of Gamma distribution of rainstorm depths,  $cm^{-1}$ ;

$h_0$  water retention capacity of surface, cm;  
 $\Gamma(\ )$  Gamma function;  
 $\gamma(\ )$  incomplete Gamma function;

$$B = \frac{1 - M}{1 + M k_v - w / \bar{e}_p} + \frac{M^2 k_v + (1 - M) w / \bar{e}_p}{2(1 + M k_v - w / \bar{e}_p)^2} \quad (A4)$$

$$C = \frac{1}{2} (M k_v - w / \bar{e}_p)^{-2} \quad (A5)$$

$$E = \frac{\alpha n_e (c - 3) K(1) \Psi(1) \phi_e}{\pi \bar{e}_p^2} s_0^{(c+5)/2} \quad (A6)$$

in which

$n_e$  effective porosity of soil;  
 $c$  pore disconnectedness index;  
 $K(1)$  saturated effective hydraulic conductivity,  $cm d^{-1}$ ;  
 $\phi_e$  dimensionless exfiltration diffusivity [Eagleson, 1978c, p. 727];  
 $w$  velocity of capillary rise to the surface from the water table,  $cm d^{-1}$ ;  
 $\Psi(1)$  matric 'bubbling pressure' head, cm (suction);  
 $s_0$  long-term average soil moisture concentration in root zone.

The value of  $\Psi(1)$  may be estimated from the soil and fluid properties using

$$\Psi(1) = \frac{\sigma_w}{\gamma_w} \left[ \frac{n_e}{k(1)\Phi} \right]^{1/2} \quad (A7)$$

where

$\sigma_w$  surface tension of water,  $dyn cm^{-1}$ ;  
 $\gamma_w$  specific weight of water,  $dyn cm^{-3}$ ;  
 $\Phi$  pore shape parameter;  
 $k(1)$  saturated intrinsic permeability,  $cm^2$ ;

and

$$\log_{10}(\Phi) = 0.150 + 0.065c + 0.035c^2 \quad (A8)$$

The diffusivity is approximated closely by

$$\phi_e = 0.3477 - 0.0731c + 0.0062 c^2 - 0.0002 c^3 \quad (A9)$$

For the fairly common conditions

$$\begin{aligned} \lambda h_0 & \ll 1 \\ \alpha / \lambda \bar{e}_p & \gg 1 \end{aligned} \quad (A10)$$

Equation (A3) may be approximated by

$$\begin{aligned} \beta_s \approx & 1 - e^{-\alpha h_0 / \bar{e}_p} \{ e^{-BE} [1 + M k_v + (2B)^{1/2} E - w / \bar{e}_p] \\ & - e^{-CE} [M k_v + (2C)^{1/2} E - w / \bar{e}_p] \\ & - (2E)^{1/2} [\gamma\left(\frac{3}{2}, CE\right) - \gamma\left(\frac{3}{2}, BE\right)] \} \quad (A11) \end{aligned}$$

The yield component is

$$\frac{E[Y_A]}{m_{PA}} = e^{-G - 2\sigma} \Gamma(\sigma + 1) \sigma^{-\sigma} + \frac{m_r k(1)}{m_{PA}} s_0^c \quad (A12)$$

where the first term on the right-hand side is surface runoff and the second is groundwater runoff, where  $m_r$  is the average length of rainy season,  $d$ , and

$$G = [K(1)/m_r] [(1 + s_0^c)/2 - w/K(1)] \quad (A13)$$

$$\sigma = \left[ \frac{5n_e(c-3)\lambda^2 K(1) \Psi(1) \phi_e}{12 \pi \delta \kappa^2} \right]^{1/3} (1 - s_0)^{2/3} \quad (A14)$$

in which  $m_i$  is the average rainstorm intensity,  $\text{cm d}^{-1}$ , and  $\phi_i$  is the dimensionless infiltration diffusivity [Eagleson, 1978c, p. 727]. P. J. Restrepo-Posada (personal communication, 1980) showed that the diffusivity can be approximated closely by

$$\phi_i = \left[ \frac{5}{3} + \frac{1}{2} (c + 1)(1 - s_0)^{1.425 - 0.0375(c+1)/2} \right]^{-1} \quad (\text{A15})$$

## NOTATION

$A$	empirical coefficient.
$B$	empirical coefficient or evapotranspiration parameter.
$C$	evapotranspiration parameter.
$c$	soil pore disconnectedness index.
$E$	dimensionless exfiltration parameter.
$E_0$	value of $E$ at which $M_0$ is maximum for a constant $k_v > 1$ .
$E_p$	potential rate of evapotranspiration, $\text{cm d}^{-1}$ .
$E_T$	rate of evapotranspiration, $\text{cm d}^{-1}$ .
$E_v$	rate of evapotranspiration from vegetation, $\text{cm d}^{-1}$ or $\text{cm yr}^{-1}$ .
$E_{pA}$	annual potential evapotranspiration, $\text{cm}$ .
$E_{p0}$	rate of potential evapotranspiration from reference crop, $\text{cm d}^{-1}$ .
$E_{TA}$	annual evapotranspiration, $\text{cm}$ .
$\bar{e}_p$	average potential rate of evaporation from bare soil, $\text{cm d}^{-1}$ .
$e_T$	rate of evapotranspiration, $\text{cm s}^{-1}$ .
$G$	gravitational infiltration parameter.
$H$	surface retention parameter.
$h_0$	water retention capacity of surface, $\text{cm}$ .
$I_g$	intensity of solar radiation at ground, $\text{cal cm}^{-2} \text{d}^{-1}$ .
$I_0$	intensity of solar radiation at top of canopy, $\text{cal cm}^{-2} \text{d}^{-1}$ .
$i$	precipitation intensity, $\text{cm s}^{-1}$ .
$K(1)$	saturated hydraulic conductivity of soil, $\text{cm d}^{-1}$ .
$k$	intrinsic permeability of soil, $\text{cm}^2$ .
$k(1)$	saturated intrinsic permeability of soil, $\text{cm}^2$ .
$k_c$	crop coefficient.
$k_v$	potential transpiration efficiency of plant species, equal to the plant coefficient.
$k_{v0}$	equilibrium plant coefficient.
$L$	leaf area index.
$M$	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, $\text{cm}$ .
$m_i$	average rainstorm intensity, $\text{cm d}^{-1}$ .
$m_{t_b}$	average time between rainstorms, $\text{d}$ .
$m_{t_r}$	average rainstorm duration, $\text{d}$ .
$m_v$	average number of interstorm periods per year.
$m_r$	average length of rainy season, $\text{d}$ .
$N_0$	net annual above-ground plant productivity, $\text{g m}^{-2}$ .
$n$	total porosity of soil.
$n_e$	effective porosity of soil.
$P_A$	annual precipitation, $\text{cm}$ .
$p$	rate of gravitational percolation, $\text{cm d}^{-1}$ .
$R_{gA}$	annual groundwater runoff, $\text{cm}$ .
$R_{sA}$	annual surface runoff, $\text{cm}$ .

$r_s$	rate of storage of surface water, $\text{cm s}^{-1}$ .
$s$	concentration of soil moisture.
$s_0$	long-term average soil moisture concentration in root zone.
$s_r$	inactive porosity of soil.
$\bar{T}_a$	average atmospheric temperature, $^{\circ}\text{C}$ .
$t$	time, $\text{d}$ or $\text{s}$ .
$w$	velocity of capillary rise from the water table, $\text{cm d}^{-1}$ .
$Y_A$	annual water yield, $\text{cm}$ .
$Z_r$	depth of root zone, $\text{cm}$ .
$\alpha$	reciprocal of average time between rainstorms, $\text{d}^{-1}$ .
$\beta$	average evapotranspiration efficiency.
$\beta_s$	average bare soil evaporation efficiency.
$\beta_v$	average transpiration efficiency.
$\gamma_w$	specific weight of water, $\text{dyn cm}^{-3}$ .
$\delta$	reciprocal of mean rainstorm duration, $\text{d}^{-1}$ .
$\kappa$	shape factor of Gamma-distributed rainstorm depths.
$\lambda$	scale factor of Gamma-distributed rainstorm depths, $\text{cm}^{-1}$ .
$\mu$	radiation extinction coefficient in canopy.
$\rho$	mass density of water, $\text{g cm}^{-3}$ .
$\sigma$	capillary infiltration parameter.
$\sigma_w$	surface tension of water, $\text{dyn cm}^{-1}$ .
$\Phi$	pore shape parameter.
$\phi_e$	dimensionless exfiltration diffusivity.
$\phi_i$	dimensionless infiltration diffusivity.
$\Psi(1)$	matric bubbling pressure head, $\text{cm}$ (suction).
$E[ ]$	expected value of [ ].
$\Delta[ ]$	finite increment of [ ].
$\gamma[ ]$	incomplete Gamma function of [ ].
$\Gamma[ ]$	Gamma function of [ ].

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