

# 19 Dynamics and Optimality in Coupled Terrestrial Energy, Water, Carbon and Nutrient Cycles

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## INTRODUCTION

The idea of ecological optimality is very attractive for those faced with the challenge of hydrological prediction in data-sparse environments. There are many alternative ways of stating what is meant by ecological optimality (some are summarized below), but for now it is enough to give a loose definition: *the ecological optimality hypothesis (EOH) holds that evolutionary selection pressures drive ecosystems towards a state of maximum utilization of available light, water and nutrient resources for the production of biomass, so that long-term net primary production (NPP) over many reproductive cycles takes the largest possible value under the constraints of available resources.* Such an hypothesis is intuitively plausible: if there are unutilized resources in the system, then some species or functional type will adapt or move in to use these resources, either co-existing with or outcompeting the under-utilizing species, and thereby increasing the overall NPP until all resources are maximally utilized. This version of an EOH also embodies the idea of an optimum ecological equilibrium attained under statistically steady resource availability from climate and non-biological soil conditions (Woodward, 1987).

The attractiveness of an EOH for hydrological prediction is that, provided it is true, it provides a powerful constraint on the NPP and the associated use of resources by the ecosystem, one of the major resources being water. Since NPP and transpiration are closely coupled, a constraint is available on transpiration, often the largest loss flux in the water balance. Transpiration is both important in its own right and also a major determinant of other loss fluxes in the water balance, through conservation of mass. In addition to practical applications in hydrological prediction, an EOH has fundamental implications in Earth system science. It provides long-term constraints on the relationship between NPP and the water cycle, which (since the water cycle is climatically and energetically constrained at large scales) places bounds on large-scale NPP. Similarly, an EOH implies a relationship between NPP and nutrient fluxes which can be used to constrain some aspects of nutrient (especially nitrogen) cycles.

Despite these attractions, most current forms of the EOH face significant difficulties. Perhaps the most important is that ecosystems exist in a time-varying environment, both because of variability in external forcing (particularly climate and human influences such as clearing, grazing and cultivation) and also because of internal dynamics associated with the growth and decay of individuals and predation.

Therefore, optimization of production must occur over averaging times long enough to account for both the growth and reproduction of individuals and also to average out the consequences of climate variability and exogenous disturbances for growth and reproduction. A second issue is that optimality is a concept that can be—and has been—applied at many hierarchical levels from individual, to single-species community, to ecosystem. It is not clear that the factors driving systems toward optimality at each of these levels are identical, other than through an origin in the evolutionary pressure of natural selection.

The aims of this chapter are to survey ecological optimality both as a principle and as a tool for hydrological prediction, and to attempt to identify some major future directions in a rich and exciting field. The next section reviews several extant lines of work, and the third section attempts to unify the main precepts of these lines in a single formulation. The fourth and fifth sections, respectively, examine the steady-state and dynamic (time-dependent) formulations of an EOH. Finally, “Looking Forward” considers future directions.

### *STRANDS OF EXISTING WORK ON ECOLOGICAL OPTIMALITY*

There are several ways that optimality principles have been formulated and applied in studies of biophysical processes. At risk of oversimplification, three strands can be identified: “plant functional”, “ecohydrological” and “resource use” optimality.

#### *1. Plant functional optimality*

Optimality approaches have been used to study the behaviour of individual plants, starting from a hypothesis that plants maximize photosynthetic carbon production over some defined time period, including a reproductive phase if this period is long enough, subject to resource (water, light and nutrient) constraints. In several specific forms, this hypothesis has been applied: (a) to derive optimal stomatal trajectories and responses to atmospheric humidity over daily time scales (Cowan 1977; Cowan & Farquhar, 1977); (b) to study the water use strategies of plants over seasonal or drought time scales (Cowan, 1982, 1986; Berninger *et al.*, 1996; Mäkelä *et al.*, 1996); (c) to determine optimal carbon and nitrogen allocation strategies between roots and shoots (Schulze *et al.*, 1983; Iwasa & Roughgarden, 1984; Johnson, 1985; Ågren & Ingestad, 1987; Hilbert, 1990; Hilbert & Reynolds, 1991); and (d) to investigate optimal reproductive growth patterns (Cohen, 1971; Vincent & Pulliam, 1980; Iwasa & Roughgarden, 1984). These investigations have achieved some significant successes in semi-quantitative prediction of phenomena such as stomatal closure in response to air dryness (saturation deficit) and increasing carbon allocation to roots in response to aridity.

#### *2. Ecohydrological optimality*

In hydrology, the term “ecological optimality” is associated almost uniquely with the work of Eagleson (1978a,b,c,d,e,f,g, 1982, 2002); see also the review of Hatton *et al.* (1997). This extensive theory uses a statistical-dynamical approach to derive optimum or climax properties of vegetation such that productivity is maximized for a given climate. In his original (1978) work, Eagleson made three hypotheses: (a) over short times (a few plant generations), vegetation canopy density equilibrates to minimize

plant water stress and maximize soil moisture (treated as a drought-stress buffer); (b) over long (successional) times, vegetation species composition adjusts to maximize soil moisture; and (c) over geological time scales, vegetation modifies soil hydraulic properties to maximize the optimal canopy density from hypothesis (a). Recently, Kerkhoff *et al.* (2004) criticized these hypotheses on both fundamental ecological grounds and for failing empirical tests, concluding that “*the poor performance of the model was probably due to the inadequate treatment of water-limited transpiration*”. However, in his recent monograph, Eagleson (2002, p.322) stated his basic hypothesis in a way which is much closer to the tenets of other work reviewed in this section: “[There exists] *a relentless evolutionary pressure toward a bioclimatically optimal vegetal state assumed to be that of maximum probability of reproductive success, which we equate to maximum seed productivity and hence, by proportion, to maximum biomass productivity*”. From this principle Eagleson (2002) used biophysical process knowledge to identify five “optimization opportunities”: optical, mechanical, thermal, hydrological and nutritional.

### 3. Resource use optimality and the resource balance hypothesis

A number of ecologists concerned with the global distribution of vegetation and terrestrial NPP (Mooney & Gulmon, 1979; Bloom *et al.*, 1985; Chapin *et al.*, 1987; Field, 1991; Field *et al.*, 1992, 1995) have adopted a “resource balance hypothesis” (RBH) which asserts that “*the combination of species sorting through ecological processes and plant acclimation through physiological, biochemical and morphological processes should tend to make all [acquired light, water and nutrient] resources equally limiting to growth*” (Field *et al.*, 1995, p.79). This resource-balance state is assumed to coincide with one in which NPP is maximized. The RBH goes beyond other statements of an EOH given above, in asserting that maximization of productivity occurs when all resources acquired by the vegetation to generate NPP (considered over the long term and at ecosystem level) are equally limiting. Experimental evidence for the RBH has come from Bloom *et al.* (1985), Chapin *et al.* (1987), Field *et al.* (1992), and recently from Shipley & Meziane (2002).

Three impressions stand out from this brief review. First, there is a high degree of convergence among different forms of the EOH in their choice of “goal function” for the optimization; all assert that plant biomass production (sometimes explicitly combined with reproduction or seed biomass production) is maximized by adaptive evolutionary selection. Second, there is a wide range of choices of the system properties which are varied to achieve optimality, depending in part upon the time scale considered: these may include stomatal conductances, allocation ratios, plant morphology, species composition, nutrient cycling and more. Third, the three identified strands of work have developed remarkably independently; few of the papers mentioned cite work from outside their own strand. The “Looking Forward” section returns to the question of the commonalities among these strands.

### A UNIFIED FRAMEWORK FOR ECOLOGICAL OPTIMALITY

At this stage it is desirable to have a formal framework which is as comprehensive as possible, so that specific predictions emerge as appropriate special cases. The starting point is to note that an EOH fundamentally involves four aspects: (a) a living system

(plant, ecosystem) obeying a set of biophysical laws such as conservation of mass and energy and the associated laws of mass and energy transfer; (b) a goal for the system, defined in all the work reviewed above as maximization of biomass or seed production; (c) a set of properties of the living system which, when varied, lead to different degrees of success in meeting the goal; and (d) an optimization process by which successful properties are selected. In nature, the optimization process is adaptive evolutionary selection. A mathematical theory for analysing problems with these four aspects is the theory of constrained optimization and optimal control, and the aspects correspond respectively to the system constraints, the goal function, the control variables and the search strategy. They fit together as follows:

Let a living system (plant or ecosystem) be characterized by a state vector (set of state variables)  $\mathbf{x}(t) = \{x_i(t)\}$ , consisting of the carbon, water, thermal energy (heat) and nutrient stores in the system at time  $t$ , expressed in mass or moles of entity (Joules in the case of energy) per individual for a plant or per unit ground area for an ecosystem. As in Raupach *et al.* (2005a,b), the rate equation governing  $x_i$  is:

$$\frac{\partial x_i}{\partial t} = \sum_j f_{ij}(\mathbf{x}, \mathbf{m}, \mathbf{p}) \quad (1)$$

where  $f_{ij}$  is the flux changing store  $i$  by process  $j$  (including flows across physical boundaries and internal biogeochemical transformations);  $\mathbf{m}(t)$  is a set of meteorological or climate forcing variables (precipitation, insolation, temperature, humidity, wind); and  $\mathbf{p}(t)$  is a set of parameters characterizing processes (such as maximum photosynthetic capacity) and soil properties (such as soil depth and hydraulic properties). Equation (1) embodies two distinct principles, the first being mass or energy conservation ( $\partial x_i / \partial t = \sum_j f_{ij}$ , summing over  $j$ ) which is always physically exact. The second is the set of “phenomenological equations”  $f_{ij} = f_{ij}(\mathbf{x}, \mathbf{m}, \mathbf{p})$  determining the dependence of the fluxes on stores ( $\mathbf{x}$ ), meteorology ( $\mathbf{m}$ ) and parameters ( $\mathbf{p}$ ). These equations are always empirical to some extent, even in strongly mechanistic models, and are dependent on the scale of the space and time averages used to define the variables in equation (1).

Equation (1) is a coupled set of differential equations determining the stores  $\mathbf{x}(t)$  and thence the fluxes  $f_{ij}(t)$ . However, it is also useful and often sufficient to solve a much simpler problem, that of finding the steady or equilibrium state of the system. This arises when the storage changes in equation (1) are much less than the fluxes, which is the case under temporal averaging in statistically steady-state conditions. Denoting long-time averaged quantities by upper-case letters, equation (1) reduces in these conditions to (for each store  $i$ ):

$$0 = \sum_j F_{ij}(\mathbf{X}, \mathbf{M}, \mathbf{P}) \quad (2)$$

Thus, in steady-state conditions, the differential governing equations reduce to a set of algebraic equations. It is important to note that the phenomenological equations determining the fluxes in equation (2) are “coarse-scale” relationships between *averaged* quantities, differing from their non-averaged or “fine-scale” counterparts in equation (1) because of nonlinearities in the fine-scale equations  $f_{ij} = f_{ij}(\mathbf{x}, \mathbf{m}, \mathbf{p})$  (Raupach *et al.*, 2005a).

The state vector  $\mathbf{x}(t)$  consists in general of all stores influencing the fluxes  $f_{ij}$  in equation (1), and thus includes carbon, water, heat and nutrient stores. As a simple

example, consider a system defined by a set of carbon stores  $\mathbf{c} = \{c_i\}$  and a single water store  $w$ , neglecting the influence of heat and nutrient stores. For this system,  $\mathbf{x} = \{\mathbf{c}, w\}$ . The carbon stores, with units  $[\text{mol C m}^{-2}]$  and including (for example) leaf, wood, root and seed carbon, are governed by:

$$\frac{dc_i}{dt} = a_i g(\mathbf{c}, w, \mathbf{m}, \mathbf{p}) - k_i c_i \quad (3)$$

where  $g(\mathbf{c}, w, \mathbf{m}, \mathbf{p})$   $[\text{mol C m}^{-2} \text{ day}^{-1}]$  is the NPP or growth carbon flux, a function of stores, meteorology and parameters;  $k_i$   $[\text{day}^{-1}]$  is the decay rate of carbon out of store  $i$ ; and  $a_i$  is the allocation coefficient for growth into carbon store  $i$ , such that  $\sum a_i = 1$  over all  $i$ . The single water store  $w$  is conveniently expressed as a relative soil moisture content  $w$  (0 in air-dry and 1 in saturated conditions), governed by:

$$W_x \frac{dw}{dt} = q_P - q_T - q_S - q_R \quad (4)$$

where  $q_P$ ,  $q_T$ ,  $q_S$  and  $q_R$   $[\text{m water d}^{-1}]$  are the water fluxes due to precipitation, transpiration, soil evaporation and runoff, and  $W_x$   $[\text{m water}]$  is the store capacity. Noting that  $q_P$  is an exogenous meteorological forcing variable and part of  $\mathbf{m}$ , the water fluxes depend like the NPP on  $(\mathbf{c}, w, \mathbf{m}, \mathbf{p})$ .

Aspect (a) of the EOH, the constraint set, is now defined. Equations (1) and (2) form the generic constraints of the problem in time-varying and steady-state conditions, respectively, and equations (3) and (4) provide examples of these constraints for a simple system. The next task is to define aspects (b) and (c), the goal function and control variables. For all the studies reviewed in the previous section, the optimization problem has the general character “maximize the biomass carbon gain (over a defined time period) for an ecosystem, a plant, or for some specific organ such as seed, by optimal adaptation of plant behaviour or attributes”. Over an interval from  $t=0$  to  $T$ , the total carbon gain is  $\sum [c_i(T) - c_i(0)]$ , and the seed carbon gain is  $c_s(T) - c_s(0)$ , where  $i=s$  is the seed carbon pool. Therefore an appropriate goal function is the weighted carbon gain:

$$J = \sum_i b_i [c_i(T) - c_i(0)] \quad (5)$$

where  $b_i$  are a set of weights for the stores  $c_i$ . If  $b_i = 1$  for all  $i$ , then  $J$  is the total carbon gain; if  $b_s = 1$  and  $b_i = 0$  for all other  $i$ , then  $J$  is the carbon gain in the seed pool only. Using equation (3), this goal function can be written for the simple model system as:

$$J = \sum_i b_i \int_0^T \frac{dc_i}{dt} dt = \sum_i b_i \int_0^T [a_i g(\mathbf{c}, w, \mathbf{m}, \mathbf{p}) - k_i c_i] dt \quad (6)$$

The optimization problem now becomes: maximize  $J$ , subject to constraints on  $\mathbf{c}$  and  $w$  from equations (3) and (4), by varying plant behaviour or attributes which can be changed by adaptation. The behaviour or attributes to be varied are the control variables of the optimization problem. They may include some of the parameters  $\mathbf{p}$  (such as properties of the stomatal conductance), the allocation ratios  $a_i$ , or the decay rates  $k_i$  (as in deciduous systems). The set of control variables will be denoted by  $\mathbf{u}(t)$ , so that  $J$  in equation (6) becomes a functional (function of a function)  $J[\mathbf{u}]$  of  $\mathbf{u}(t)$ , to be maximized by varying  $\mathbf{u}(t)$ .

If the problem is reduced from its full time-dependent form to the steady-state form by taking a time average as in equation (2), then the goal function needs to be modified because  $dc_i/dt = 0$  in the steady state, so  $J$  in equation (6) is zero. The logical steady-state equivalent is to require maximization of the time-averaged production  $G(\mathbf{C}, \mathbf{W}, \mathbf{M}, \mathbf{P})$ , subject to the constraints of equation (2). The average production must be expressed in terms of time-averaged quantities since only these are available in a steady-state analysis. In general, the coarse-scale phenomenological equation specifying the averaged  $G(\mathbf{C}, \mathbf{W}, \mathbf{M}, \mathbf{P})$  is not the same as that for the fine-scale (short-term) production  $g(\mathbf{c}, \mathbf{w}, \mathbf{m}, \mathbf{p})$  (Raupach *et al.* 2005a).

The last aspect (d) of the EOH is the search strategy for finding the optimal control variables  $\mathbf{u}(t)$  which maximize  $J$ . In nature, this strategy is adaptive evolution. It is possible to replicate this process algorithmically through the use of genetic algorithms, an approach with significant advantages including the ability to find a global maximum in  $J$  when there are multiple local maxima in  $\mathbf{u}$  space. However, this paper is based on long-standing alternatives which yield opportunities for analytical insight, based on the theories of constrained optimization, calculus of variations and optimal control. The following two sections survey the application of these theories to steady-state and dynamic (time-dependent) ecological optimality, respectively. In each case a mathematical theorem is outlined and then applied.

### ECOLOGICAL OPTIMALITY IN THE STEADY STATE

The necessary mathematical foundation is a basic theorem found in many textbooks on mathematical analysis, which will be referred to as the constrained optimization (CO) theorem.

*The constrained optimization (CO) theorem* The aim is to find a vector of  $N_k$  control variables,  $\mathbf{u} = \{u_k\}$ , which locally extremizes (maximizes or minimizes) a given scalar function  $j(\mathbf{u})$ . If there are no constraints on the allowable  $\mathbf{u}$  (and if  $j(\mathbf{u})$  is smooth enough) the problem is easy: find the  $u_k$  satisfying the  $K$  equations  $\partial j / \partial u_k = 0$ . However, suppose also that there are  $N_m$  constraints on  $\mathbf{u}$ , of the form  $f_m(\mathbf{u}) = 0$  (where  $M < K$ , otherwise the constraints fix  $\mathbf{u}$  completely). The problem is now harder, but it is solved by introducing  $N_m$  “undetermined Lagrange multipliers”  $\lambda_m$  and forming the Lagrangian  $L(\mathbf{u}, \boldsymbol{\lambda}) = j(\mathbf{u}) + \sum \lambda_m f_m(\mathbf{u})$ . The CO theorem states that the control vector  $\mathbf{u}$  which extremizes  $j(\mathbf{u})$ , subject to constraints  $f_m(\mathbf{u}) = 0$ , is obtained by solving the *unconstrained* problem of extremizing  $L(\mathbf{u}, \boldsymbol{\lambda})$  in both  $\mathbf{u}$  and  $\boldsymbol{\lambda}$ ; that is, solving the  $N_k + N_m$  equations  $\partial L / \partial u_k = 0$  and  $\partial L / \partial \lambda_m = 0$  for the  $N_k + N_m$  unknowns  $u_k$  and  $\lambda_m$ . The resulting  $u_k$  are the optimal values. For proofs and examples, see Mathews & Walker (1964), Vagners (1974) and Pinch (1993). The  $N_m$  equations  $\partial L / \partial \lambda_m = 0$  imply that  $f_m(\mathbf{u}) = 0$ , and thus embody the constraints.

To apply the CO theorem to a basic problem in ecological optimality, consider a system in which the steady-state NPP  $G(\mathbf{C}, \mathbf{W}, \mathbf{M}, \mathbf{P})$  is a known function, and with known steady-state decay rates  $K_i$  for the carbon pools (using upper-case letters for time-averaged quantities). The aim is to find the carbon allocation ratios  $A_i$  which maximize  $G$ , and thence  $G$  itself, the carbon stores  $C_i$ , and the water fluxes which depend on vegetation ( $Q_T$  and  $Q_S$ ), at this optimum point.

From equation (3), the steady-state carbon balance for each store  $C_i$  is  $A_i G - K_i C_i = 0$ . The constraint is that the total mass of carbon is at steady state. Summing over all  $i$ , this becomes:

$$G - \sum_i K_i C_i = G - \mathbf{K} \cdot \mathbf{C} = 0 \quad (7)$$

(since  $\sum A_i = 1$ ). The control variables ( $\mathbf{u}$ ) are  $A_i$ . At steady state these are related to the stores by  $C_i = A_i G / K_i$ , so the problem of finding  $A_i$  is equivalent to that of finding the stores  $C_i$  that maximise  $G$ , subject to Equation (7) as a constraint. Thus reformulated, the control vector  $\mathbf{u}$  in the problem becomes  $\mathbf{C}$ . The Lagrangian in the CO theorem is then given by:

$$L(\mathbf{C}, \lambda) = G(\mathbf{C}) + \lambda[G(\mathbf{C}) - \mathbf{K} \cdot \mathbf{C}] \quad (8)$$

where the function to be maximized is  $G(\mathbf{C})$  (with only the control variables  $\mathbf{C}$  shown explicitly as independent variables) and where there is one Lagrange multiplier  $\lambda$ , since there is only one constraint. Applying the CO theorem, the optimum  $\mathbf{C}$  occurs when  $\partial L / \partial C_i = 0$  and  $\partial L / \partial \lambda = 0$ . The latter equation simply restates the constraint, but the former shows that at the optimum:

$$0 = \frac{\partial G}{\partial C_i} + \lambda \frac{[G - \mathbf{K} \cdot \mathbf{C}]}{\partial C_i} \quad \text{or} \quad \frac{\partial G}{\partial C_i} = \left( \frac{\lambda}{\lambda + 1} \right) K_i \quad (9)$$

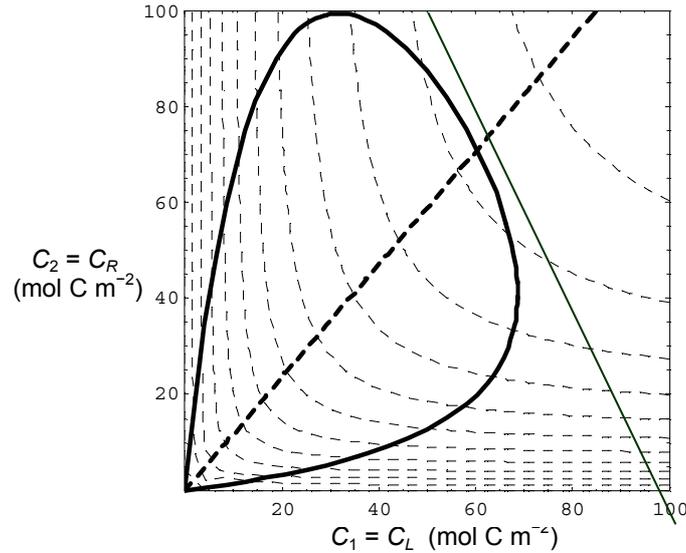
Since  $\partial G / \partial C_i$  is a known function of  $\mathbf{C}$ , equation (9) determines the optimum  $C_i(\lambda)$  as a function of  $\lambda$  (which is as yet unknown). The appropriate value of  $\lambda$ , and thence the solution  $C_i(\lambda)$ , is found by requiring that  $C_i(\lambda)$  satisfy the constraint, equation (7).

Figure 18.1 shows a geometrical interpretation of this solution, considering a two-dimensional (2-D) system with just two carbon pools ( $C_1, C_2$ ) so that representation on a plane is possible. A set of contour surfaces  $G(\mathbf{C}) = \text{constant}$  are shown (these are lines in 2-D), along with the surface on which the constraint, equation (7), is satisfied (again a line in 2-D). The optimum solution has to lie on the constraint surface. The second part of equation (9) shows that it occurs where the constraint surface intersects a line along which the gradient  $\partial G / \partial C_i$  is parallel to the vector of decay rates,  $K_i$ . This line is also shown; its intersection with the constraint surface is the optimum solution. The first of equation (9) indicates another geometrical interpretation (Pinch, 1993): the optimum occurs where the gradients of the goal function ( $G$ ) and the constraint function ( $G - \mathbf{K} \cdot \mathbf{C}$ ) are parallel, that is, where the constraint surface is tangent to the contours of the goal function.

The above result is general for any NPP  $G(\mathbf{C}, \mathbf{W}, \mathbf{M}, \mathbf{P})$ . To make explicit predictions for the allocation ratios, consider a 2D system in which the carbon pools are leaf ( $C_L$ ) and root ( $C_R$ ), so that  $\mathbf{C} = (C_1, C_2) = (C_L, C_R)$ . A model is required for the NPP; this must represent explicitly the dependence of NPP on both leaf biomass ( $C_L$ ) and root biomass ( $C_R$ ), and also the effects of the meteorological forcing variables which influence NPP, assumed here to be light and water supply only. For illustrative calculations, a very simple NPP model is used in which  $G$  is assumed to be the inverse sum of a light-limited NPP  $G_{QLim}$  and a water-limited NPP  $G_{WLim}$ :

$$1/G = 1/G_{QLim} + 1/G_{WLim} \quad (10)$$

where  $G_{QLim}$  is proportional to the incident flux of photosynthetically active radiation



**Fig.18.1** Geometrical interpretation of the optimal (maximum-growth) solution for carbon pools  $(C_1, C_2) = (C_L, C_R) = (\text{leaf}, \text{root})$ . The dashed lines are the contours of the NPP  $G(C)$  on the  $(C_1, C_2)$  plane. The solid heavy line is the set of points  $(C_1, C_2)$  on which the carbon mass balance constraint, equation (7), is satisfied. The dashed heavy line is the set of points  $(C_1, C_2)$  on which the gradient  $\partial G/\partial C_i$  is parallel to the vector of decay rates,  $K_i$ . The optimum solution is at the intersection of the solid and dashed heavy lines, and is also the point at which the tangent to the constraint line (shown as a light solid line) is parallel to the contours of  $G(C)$ . The contours for  $G(C)$  are constructed using equation (12), with relative soil moisture  $W = 0.5$  and other parameters as specified in the caption for Fig. 18.2. With these parameters,  $G = 0.26 \text{ mol C m}^{-2} \text{ day}^{-1}$  at the optimum point. Contours are at intervals of  $0.025 \text{ mol C m}^{-2} \text{ day}^{-1}$ .

(PAR), and  $G_{WLim}$  is proportional to the relative soil water content  $W$ . This form has the desirable properties that  $G$  approaches zero as either light or water supply approaches zero ( $G \rightarrow 0$  as  $G_{QLim} \rightarrow 0$  or  $G_{WLim} \rightarrow 0$ ), and  $G$  approaches the light-limited (or water-limited) value when the water-limited (or light-limited) value becomes large ( $G \rightarrow G_{QLim}$  as  $G_{WLim} \rightarrow \infty$ , and  $G \rightarrow G_{WLim}$  as  $G_{QLim} \rightarrow \infty$ ). Simple forms for  $G_{QLim}$  and  $G_{WLim}$  are:

$$G_{QLim} = \left( \frac{C_L}{C_L + C_{L0}} \right) \alpha_Q F_{Qx}; \quad G_{WLim} = \left( \frac{C_R}{C_R + C_{R0}} \right) \alpha_W F_{Wx} W \quad (11)$$

where  $\alpha_Q$  [ $\text{mol C mol PAR}^{-1}$ ] is a light use efficiency;  $\alpha_W$  [ $\text{mol C mol water}^{-1}$ ] is a water use efficiency;  $F_{Qx}$  [ $\text{mol PAR m}^{-2} \text{ day}^{-1}$ ] is the incident flux of photosynthetically active radiation (PAR);  $F_{Wx}$  [ $\text{mol water m}^{-2} \text{ day}^{-1}$ ] is a proportionality constant relating the soil-limited transpiration flux of water to the time-average relative soil moisture  $W$  (so that in water-limited conditions, transpiration [ $\text{mol water m}^{-2} \text{ day}^{-1}$ ] is  $F_{Wx}W$ ); and  $C_{L0}$  and  $C_{R0}$  are scales which specify the values for  $C_L$  and  $C_R$  at which lack of leaf and root biomass limit light and water capture, respectively. The factors  $C_L/(C_L + C_{L0})$  and

$C_R/(C_R + C_{R0})$ , respectively, account for limitation of light uptake by lack of leaf and water uptake by lack of root. The NPP is therefore given by:

$$G(C_L, C_R) = \left[ \left( \frac{C_L + C_{L0}}{C_L} \right) \frac{1}{\alpha_Q F_{Qx}} + \left( \frac{C_R + C_{R0}}{C_R} \right) \frac{1}{\alpha_W F_{Wx} W} \right]^{-1} \quad (12)$$

This model is not justified here, simply being used as a plausible description of the dependence of NPP on  $C_L$ ,  $C_R$  and light and water supply. It yields the contours of  $G(C_L, C_R)$  in Fig. 18.1.

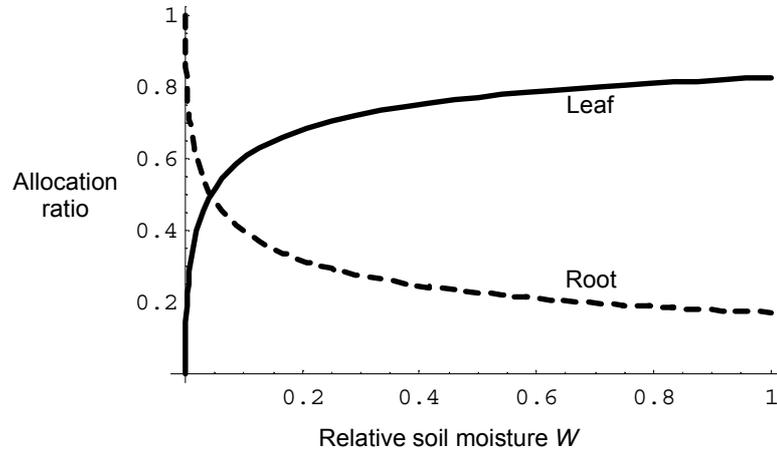
Explicit allocation predictions now follow from the requirement of equation (9). Using equation (12) to specify  $G$ , this requirement is:

$$\left( \frac{\partial G}{\partial C_L}, \frac{\partial G}{\partial C_R} \right) = G^2 \left( \frac{C_{L0}}{\alpha_Q F_{Qx} C_L^2}, \frac{C_{R0}}{\alpha_W F_{Wx} W C_R^2} \right) \text{ parallel to } (K_L, K_R) \quad (13)$$

Using the fact that  $C_L = A_L G / K_L$  and  $C_R = A_R G / K_R$  at equilibrium, a simple solution is obtained for the allocation ratios  $A_L$  and  $A_R$ :

$$A_L = \left( 1 + \sqrt{\frac{F_{Qx}}{F_{Wx} W} \frac{\alpha_Q}{\alpha_W} \frac{C_{R0}}{C_{L0}} \frac{K_R}{K_L}} \right)^{-1}; \quad A_R = 1 - A_L \quad (14)$$

Figure 18.2 shows the behaviour of this solution as the equilibrium relative soil moisture  $W$  is varied. With decreasing  $W$  there is progressively more allocation of carbon to root as the vegetation responds to aridity by investing more biomass in water-harvesting organs. This reproduces the known ecological trend.



**Fig. 18.2** Allocation ratios predicted by equation (14) as a function of equilibrium relative soil moisture  $W$ . Parameters in equation (14) and the model for NPP  $G(C)$ , equation (12), are: light use efficiency  $\alpha_Q = 0.04 \text{ mol C mol PAR}^{-1}$ ; water use efficiency  $\alpha_W = 0.005 \text{ mol C mol water}^{-1}$ ; incident PAR flux  $F_{Qx} = 40 \text{ mol PAR m}^{-2} \text{ day}^{-1}$ ; proportionality constant relating soil-limited transpiration to relative water content  $F_{Wx} = 925 \text{ mol water m}^{-2} \text{ day}^{-1}$ ; scales for limitation of NPP and transpiration by lack of leaf and root,  $C_{L0} = 40 \text{ mol C m}^{-2}$  and  $C_{R0} = 40 \text{ mol C m}^{-2}$ ; leaf and root pool decay rates  $K_L = 1 \text{ year}^{-1}$  and  $K_R = 0.5 \text{ year}^{-1}$ .

### ECOLOGICAL OPTIMALITY IN DYNAMIC SYSTEMS

In dynamic or time-evolving systems the opportunities for optimization are much richer than in steady-state systems. The underpinning analytical framework is derived from the theories of calculus of variations and optimal control. Calculus of variations, originated in the eighteenth century by Euler and Lagrange, has the aim of finding a function  $\mathbf{u}(t)$  which extremizes an integral  $J[\mathbf{u}]$  akin to equation (6), subject to constraints akin to equation (1). In efforts to apply this theory to problems of spacecraft navigation in the 1950s, a central difficulty emerged: all functions in the calculus of variations need strong smoothness properties for the basic arguments to work, whereas control functions  $\mathbf{u}(t)$  for many real-world problems (including ecological optimality!) turn out not to be smooth at all. The generalization to non-smooth functions is called optimal control theory, one of its main theorems being the Pontryagin Maximum Principle (PMP) developed in Russia in the 1940s and 1950s. This is the theorem needed here. Before summarizing the PMP, it should be noted that the term “control theory” is often misunderstood as implying some sort of central command mechanism. In fact the theory makes no such assumption: it merely seeks to identify best possible trajectories and makes no statements about how they are to be achieved. In this sense the word “control” is a misnomer arising from the engineering origins of the theory, and for ecological purposes the theory would be better construed as “time-dependent constrained optimization theory”.

*The Pontryagin Maximum Principle (PMP)* Let  $\mathbf{x}(t) = \{x_m(t)\}$  be a vector of  $N_m$  state variables, obeying dynamic constraints specified by the given differential equations:

$$d\mathbf{x}/dt = \mathbf{f}(\mathbf{x}(t), \mathbf{u}(t)); \quad \mathbf{x}(0) = \mathbf{x}_0 \quad (15)$$

where  $\mathbf{u}(t) = \{u_k(t)\}$  is a set of  $N_k$  time-dependent control variables. The aim is to find the functions  $\mathbf{u}(t)$  which maximize a goal function  $J$ , defined as the integral over the time interval  $0 \leq t \leq T$  of a specified scalar function  $j(\mathbf{x}, \mathbf{u})$ :

$$J[\mathbf{u}] = \int_0^T j(\mathbf{x}(t), \mathbf{u}(t)) dt \quad (16)$$

The PMP states that the optimizing  $\mathbf{u}(t)$  are given by maximizing the Hamiltonian:

$$h(\mathbf{x}, \mathbf{u}, \boldsymbol{\lambda}) = j(\mathbf{x}, \mathbf{u}) + \sum_m \lambda_m f_m(\mathbf{x}, \mathbf{u}) \quad (17)$$

with respect to the control variables  $\mathbf{u}(t)$  at each instant  $t$ , where  $\mathbf{x}(t)$  and  $\boldsymbol{\lambda}(t)$  obey the equations:

$$\frac{dx_m}{dt} = \frac{\partial h}{\partial \lambda_m} \quad (\text{with } \mathbf{x}(0) = \mathbf{x}_0); \quad \frac{d\lambda_m}{dt} = -\frac{\partial h}{\partial x_m} \quad (\text{with } \boldsymbol{\lambda}(T) = 0) \quad (18)$$

These two sets of equations are called the state and costate (or dual, or adjoint) equations, and the  $N_m$  variables  $\boldsymbol{\lambda}(t) = \{\lambda_m(t)\}$  are called the costate (or dual, or adjoint) variables. They are analogous to the Lagrange multipliers in the CO theorem. One can interpret  $\lambda_m(t)$  as the marginal benefit to the overall goal function  $J$  of a change in  $x_m(t)$  induced by a small perturbation  $\delta\mathbf{u}$  in the control variables at time  $t$  (Iwasa & Roughgarden 1984). For accounts of the underlying mathematics, see Pinch (1993) and Casti (2000). The PMP has predictive applications in physics, engineering, economics,

ecology and other fields, and important procedural applications in data assimilation and model-data synthesis (Raupach *et al.*, 2005b).

The PMP requires a three-step process to find an optimum trajectory: (a) find  $\mathbf{x}(t)$  by integrating the state equations forward in time from  $t = 0$  to  $T$ ; (b) find  $\boldsymbol{\lambda}(t)$  by integrating the costate equations backward in time from  $t = T$  to 0 (since the boundary condition is at  $t = T$ ); and (c) find the control variables  $\mathbf{u}(t)$  which maximize the Hamiltonian  $h(\mathbf{x}, \mathbf{u}, \boldsymbol{\lambda})$  at each instant. It is crucial that  $\mathbf{u}(t)$  need not be continuous. An important case in which  $\mathbf{u}(t)$  is not continuous arises when the Hamiltonian is linear in  $\mathbf{u}$ , which happens if  $j(\mathbf{x}, \mathbf{u})$  and  $f_m(\mathbf{x}, \mathbf{u})$  are linear in  $\mathbf{u}$ . In this case the components of the optimum  $\mathbf{u}(t)$  jump discontinuously between their minimum and maximum possible values without taking any values in between, a situation known as “bang-bang control” (Pinch, 1993; Casti, 2000). For example, suppose that components of  $\mathbf{u}(t)$  can vary between 0 and 1, and that  $h$  is a linear combination  $\sum h_k u_k$  of these components (where the  $h_k$  are functions of  $\mathbf{x}$  and  $\boldsymbol{\lambda}$ ). The choice of  $\mathbf{u}$  that maximizes  $h$  is to set  $u_k = 1$  for the  $k$  value corresponding to the largest of the  $h_k$ , and  $u_k = 0$  for all other  $k$  values.

As an ecological example, consider the problem of choosing time-dependent allocation coefficients  $a_i(t)$  to maximize the growth integral  $J$  defined by equation (6). The state variables ( $\mathbf{x}$  in the PMP) are the carbon stores  $\mathbf{c}(t)$ ; the dynamic constraints ( $f_m$ ) are given by equation (3); the control vector ( $\mathbf{u}$ ) is the vector of allocation coefficients  $\mathbf{a}(t) = \{a_i(t)\}$ ; and the integrand ( $j$ ) of the integral goal function ( $J$ ) is the weighted growth  $\sum b_i(a_i g - k_i c_i)$ , where  $b_i$  are weights defined in equation (5). The Hamiltonian for this system is:

$$h(\mathbf{c}, \mathbf{a}, \boldsymbol{\lambda}) = (b_i + \lambda_i)(a_i g(\mathbf{c}, w, \mathbf{m}, \mathbf{p}) - k_i c_i) \quad (19)$$

Since this is linear in the control variables  $a_i$ , the control has “bang-bang” character. Given that  $0 \leq a_i \leq 1$  and  $\sum a_i = 1$ , it follows from the PMP that the vector  $\mathbf{a}(t) = \{a_i(t)\}$  which maximizes  $h$  with respect to  $\mathbf{a}$  at each instant  $t$  is of the form  $(0, \dots, 0, 1, 0, \dots, 0)$ , where the single component 1 is associated with the store  $i$  for which  $(b_i + \lambda_i)$  is largest. This depends on the costate variables or marginal benefits  $\lambda_i(t)$ , which are determined by the costate or adjoint equation  $d\lambda_i/dt = -\partial h/\partial c_i$ . The  $\lambda_i(t)$  determine which store this is, and in control theory are called switching functions (Pinch, 1993).

Even without solving for the  $\lambda_i(t)$ , two conclusions follow at this point. First, all carbon goes instantaneously to the carbon store (or organ, such as leaf, root, ...) conferring the greatest instantaneous growth benefit (Iwasa & Roughgarden, 1984), which varies in time among the possible choices in response to changing external conditions. This dynamic view of allocation is quite different from the steady-state view summarized in the previous section: the trajectories of  $a_i(t)$  are not simply the steady-state  $A_i$  with the addition of a perturbation, but rather the  $A_i$  are the long-time averages of discontinuous  $a_i(t)$  which switch between 0 and 1. In fact,  $A_i$  is the time fraction for which  $a_i(t)$  is 1, or  $b_i + \lambda_i(t)$  is the largest component of the vector  $\mathbf{b} + \boldsymbol{\lambda}(t)$ . This is also the fraction of time for which growth is limited by the gathering of resources through carbon store  $i$ .

Second, by defining the goal function as maximization of seed carbon ( $b_i = 1$  for seed and 0 for other stores), it follows as a particular case of the first conclusion that the optimal strategy for investment in seed is to switch entirely to seed production at some point in the developmental cycle, as for instance in the haying-off of grasses in

an annual cycle. This conclusion was reached by Cohen (1971) and Vincent (1980) and formalized by Iwasa & Roughgarden (1984) using the PMP as outlined here.

### **LOOKING FORWARD**

This final section is a personal perspective on where ecological optimality stands now and is heading in the future, particularly from the standpoint of hydrological prediction. The discussion covers both the central hypothesis, the EOH expressed in various forms and various scales, and also the ensuing theoretical and predictive frameworks.

Starting with the present position, a major achievement from all three strands reviewed initially above (optimality in plant function, ecohydrology and resource use) has been the establishment and formalization of a holistic perspective. In this, the nonliving components of the terrestrial biosphere (such as transfer processes in water, soil and air) interact dynamically with the living components (ecosystems and the organisms of which they are composed). Thus, hydrology is more than fluid mechanics and ecology is more than biological processes writ large. A systematic framework for describing and predicting the dynamics of this richly coupled system is emerging, but there is a long way to go. Four future challenges are identified here.

#### **1. *Extending the state space and the level of coupling***

In the examples in this paper, the state variables defining the system have been carbon and water stores and only the carbon stores have been explicitly subjected to optimization, with the consequences of optimality for other stores and processes (in particular, water) being expressed through the phenomenological equations. In the future, it is important to develop a more comprehensive view of the coupled system and the opportunities for adaptive evolution to maximize overall production. This will involve including nutrients explicitly in the state space, and resolving all stores more precisely; for example, resolving water stores into soil layers or compartments defined by ease of water extraction, and carbon and nutrient stores into physically or biochemically defined fractions as in many terrestrial biosphere models which do not use optimality concepts (Raupach *et al.*, 2005a). There are many possibilities for application of an EOH to such models; for example, investigations of: (a) the nutrient balance of ecosystems and the fraction of system resource devoted to nitrogen fixation by indigenous legumes; (b) the interactions between water, biomass and nutrients; and (c) growth, allocation and morphology both above and below ground. Eagleson (2002) has already explored some aspects of these directions in a steady-state framework, for instance the responses of plant and leaf form to climate. A further application of optimality hypotheses in coupled terrestrial biosphere modelling is to aid in parameter estimation, as some parameters are converted into control variables and constrained by the optimization.

#### **2. *Further developing the dynamic perspective***

Perhaps the most important specific challenge raised in this chapter is to develop the implications of optimality hypotheses in dynamic (time-dependent) systems. The examples suggest that profound changes in understanding and outlook, and thence predictive ability, can be brought about by moving from a steady-state to a dynamic or time-evolving description of the system. Many important attributes of plant and

ecosystem function are invisible in a steady-state description and can only be understood and predicted by considering changes through time; examples include reproduction, responses to climate variability, and responses to episodic disturbances such as fire and flood. The ways that plants and ecosystems accommodate these factors are central to their long-term survival and fitness, so it is crucial that they be included in optimality analyses.

### 3. *Developing new techniques for dynamic optimization*

There are significant technical challenges in solving dynamic optimization problems. Optimal control theory (as outlined in the previous section) is one possible approach that has been explored to some extent, and which offers promise for substantial further development. One route worthy of exploration is the use of stochastic optimal control theory, in which state, costate and control variables all become random processes described by probability distributions (rather than deterministic processes as in the above sketch of the PMP) and the goal function becomes the maximization of a probability, for example for long-term survival. An apparently quite different approach is the use of evolutionary computation (such as genetic algorithms or agent based modelling) to model real-world evolutionary processes. This approach has appeal in that it directly models the survival-based selection filter in adaptive evolution toward an optimum. However, it lacks an analytical foundation comparable to that established for constrained optimisation theory in any of its forms, which can make it nearly as difficult to understand why a model exhibits some behaviour as it is to understand why nature behaves as it does. Evolutionary computation looks and feels to be only distantly related to analytic optimal control theory or dynamical systems theory (upon which control theory is built), but there are basic connections between the two approaches. One (evolutionary computation) describes individuals explicitly and infers population behaviour by summing over all individual behaviours, while the other (dynamical systems and optimal control) models population behaviour directly in terms of the evolution of probability distributions or (in deterministic versions) trajectories of mean quantities. The theory of stochastic processes offers tools for relating and unifying these perspectives, at least for simple systems. A worthwhile endeavour is to explore the implications of such an approach in ecological optimality.

### 4. *Understanding dynamic optimality in relation to resilience and adaptive capacity*

The dynamic perspective on ecological optimality is important not only because it offers the potential of greater predictive capacity as suggested in point 2 above, but also for a yet more fundamental reason. The emergence of complexity in systems governed by relatively simple laws has been one of the defining scientific problems of the period since around 1980, and is likely to continue to be so (see for example Waldrop, 1994, Dennett, 1995, Holland, 1998). Systems such as landscapes, ecosystems, ant colonies, crowds, economies and societies are increasingly being seen as examples of “complex adaptive systems” (CAS) in which the emergence of complexity and organization is a common thread with universal properties. Among these properties are the ability to store and propagate information, growth-decay-renewal cycles which offer the possibility for adaptive evolution, and the consequent emergence of self-organization at system level. In systems with this self-organizing

ability, nothing is static or steady-state: adaptations by one part of the system continually change the “fitness landscape” for other parts, inducing adaptive evolution in those parts. To describe such systems, the CAS-oriented ecological community is developing the ideas of “resilience” (the ability of a whole system or a component part to withstand external shocks without a catastrophic change in state) and “adaptive capacity” (the ability to respond to changes in external conditions through adaptive evolution).

The CAS perspective has several implications for ecological optimality. First, it provides context and limits for an ecological optimality hypothesis. Optimality is a useful concept only if the time scale needed for evolution towards a hypothesized optimal state is substantially less than the time scale for system disturbance or changes in the “system rules”, embodied, for example, in the phenomenological equations in equation (1). Second, the CAS view focuses attention on the spatial or system scale at which an EOH is applied. Optimality requirements (through the goal of maximization of long-term production) can be defined both for individuals and for the ecosystem as a whole, but it is evident that in a dynamically evolving, multi-component system, these two requirements do not generally coincide. Finally, the CAS view highlights the evolutionary tension between short-term and long-term optimality, or between production and survival for the component parts of a system which is both internally evolving and also subject to variable external forcing. The existence of multiple strategies for resolving this tension is one of the main drivers of diversification. Ecological optimality theory, especially in its dynamic forms, is well placed to contribute to better quantitative understanding of these fundamental questions. Thus, the practical task of hydrological prediction in ungauged catchments, through the use of an ecological optimality hypothesis, is connected with some of the most fundamental challenges facing contemporary science.

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