

Maximum entropy production and plant optimization theories

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Plant ecologists have proposed a variety of optimization theories to explain the adaptive behaviour and evolution of plants from the perspective of natural selection ('survival of the fittest'). Optimization theories identify some objective function—such as shoot or canopy photosynthesis, or growth rate—which is maximized with respect to one or more plant functional traits. However, the link between these objective functions and individual plant fitness is seldom quantified and there remains some uncertainty about the most appropriate choice of objective function to use. Here, plants are viewed from an alternative thermodynamic perspective, as members of a wider class of non-equilibrium systems for which maximum entropy production (MEP) has been proposed as a common theoretical principle. I show how MEP unifies different plant optimization theories that have been proposed previously on the basis of ad hoc measures of individual fitness—the different objective functions of these theories emerge as examples of entropy production on different spatio-temporal scales. The proposed statistical explanation of MEP, that states of MEP are by far the most probable ones, suggests a new and extended paradigm for biological evolution—'survival of the likeliest'—which applies from biomacromolecules to ecosystems, not just to individuals.

Keywords: entropy production; natural selection; optimization; plants

1. INTRODUCTION

Just as large-scale, parameter-intensive global circulation models currently dominate modelling of climate dynamics, modelling of plant and terrestrial ecosystem dynamics is currently dominated by complex, numerical simulation models that attempt to represent explicitly the many physical, successional and biogeochemical processes governing plant and ecosystem function. To some extent, this approach reflects the demand from the global change research community for land-surface models that operate over a wide range of vegetation types, environments and time scales.

In this 'bottom-up' approach, plausible assumptions are introduced about each process for each plant type, requiring typically hundreds of parameters to be specified, few of which are identifiable from available data (e.g. Wang *et al.* 2001). These processes are then coupled together in various ways, leading to a wide range of model structures. Crucially, when it comes to modelling the adaptive responses of plants to global change—e.g. the responses of stomatal conductance, plant nitrogen content, leaf biomass and leaf–root growth allocation to changes in CO₂, nitrogen and water availability—complex models generally offer no explanation of those responses; they are usually represented empirically, if at all. Consequently, uncertainties in model parameter values, differences

among model structures and the empirical treatment or omission of key adaptive plant processes have led to a great divergence in the predicted responses of complex vegetation models to elevated [CO₂] (e.g. Cramer *et al.* 2001), nitrogen (N) enrichment (e.g. Levy *et al.* 2004) and combined changes in [CO₂], precipitation and temperature (e.g. Luo *et al.* 2008).

Theories of optimal plant function offer an alternative 'top-down' approach to modelling in plant ecology (e.g. Givnish 1986; Kull 2002; Mäkelä *et al.* 2002; Dewar *et al.* 2009; Schymanski *et al.* 2009). Optimization models identify an apparent goal or objective function F that is maximized with respect to one or more plant functional traits f . The maximization of F is usually subjected to one or more physiological or environmental constraints C . The advantage of this approach is that it avoids the need for an explicit sub-model for f with its attendant parameters; instead, f is simply determined by the optimality condition that F is stationary with respect to variations in f permitted by the constraints C .

Functional traits to which the optimization approach has been applied include stomatal conductance (e.g. Cowan & Farquhar 1977), leaf and canopy N content (e.g. Dewar 1996; Haxeltine & Prentice 1996), shoot/root biomass ratio (e.g. Reynolds & Thornley 1982), N allocation within canopies (e.g. Field 1983), allocation between height and diameter growth in trees (Mäkelä & Sievänen 1992) and leaf-area index (e.g. McMurtrie 1985; Franklin & Ågren 2002). Unlike complex vegetation models, optimization models explain—not only qualitatively but also quantitatively—many of the plant trait responses to changes in CO₂, N and water supply observed

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in multiple-resource manipulation experiments and other empirical studies as consequences of the maximization of various objective functions (e.g. Dewar *et al.* 2009). While this is encouraging, optimization models have yet to be adopted as mainstream modelling tools in global change research.

One reason for this might be because we do not yet have an unambiguous answer to the key question: What do plants maximize? Often the objective function F is proposed as some proxy for individual fitness—such as shoot or canopy photosynthesis, net primary productivity or net growth rate (e.g. Dewar 1996; Dewar *et al.* 1998; Ackerly 1999; Hikosaka 2003; Anten 2005; Franklin 2007; Mäkelä *et al.* 2008; McMurtrie *et al.* 2008; Dewar *et al.* 2009)—although the link with individual fitness is seldom quantified and usually only a verbal justification of F is offered. In particular, if natural selection operates uniquely at the level of individuals, the use of canopy-scale objective functions (e.g. canopy photosynthesis) may be called into question. As a result, there remains some uncertainty about the most appropriate choice of objective function to use.

Recently, however, an alternative thermodynamic perspective on biological adaptation and evolution has emerged (Dewar 2004; Whitfield 2005, 2007; Martyushev & Seleznev 2006), which identifies a fundamental objective function based on entropy concepts. Within this perspective, living systems are viewed as examples of a wider class of non-equilibrium structures—including non-living systems such as growing crystals and weather cyclones—that import energy in one form and export it in a higher entropy form. The hypothesis of maximum entropy production (MEP) conjectures that these systems self-organize (adapt, evolve) under given constraints so as to maximize this rate of entropic export.

The theoretical basis of MEP remains a subject of open debate (e.g. Dewar 2004, 2009; Martyushev & Seleznev 2006; Bruers 2007; Grinstein & Linsker 2007; Niven 2009). One proposition is that MEP has a statistical explanation (Dewar 2003, 2005, 2009): when a system is forced out of thermodynamic equilibrium, the non-equilibrium state of MEP is selected simply because it is by far the most probable one—that is, the MEP state can be realized microscopically in an overwhelmingly greater number of ways than any other non-equilibrium state. In this sense, MEP is a statistical principle, rather than a physical principle open to experimental falsification (Dewar 2009).

MEP has previously been applied to biological systems, for example, the evolution of biomacromolecules (e.g. Dewar *et al.* 2006) and food web functioning in detrital-based ecosystems (Meysman & Bruers 2007). In this paper, I apply MEP to plant function. The aim is to demonstrate how MEP unifies and extends various plant optimization theories that have been proposed previously on the basis of ad hoc natural selection arguments ('survival of the fittest'). Specifically, using simple models of the carbon balance of plants and ecosystems, I show that the different objective functions of these theories emerge as examples of entropy production on different spatio-temporal

scales. MEP thus predicts optimal plant behaviour that is reasonable from the perspective of natural selection, but, in addition, offers a novel statistical reinterpretation of that behaviour—'survival of the likeliest' (Whitfield 2007)—which extends beyond individual plants to vegetation canopies and whole ecosystems.

The paper is organized as follows. Section 2 outlines the basic formalism for calculating the rate of chemical entropy production in plants and ecosystems (σ_{chem}), involving a simplifying approximation that the system is in a quasi-steady state. In §3, MEP is applied successively to three systems that can be considered to be in a quasi-steady state on different time scales. In each case, the expression for σ_{chem} is related to the objective functions of previously proposed plant optimization theories, and a brief illustration is given of how MEP can lead to realistic optimal plant function. Section 4 presents some conclusions.

2. CHEMICAL ENTROPY PRODUCTION BY PLANTS AND ECOSYSTEMS

The instantaneous rate of chemical entropy production (σ_{chem} , $\text{JK}^{-1}\text{s}^{-1}$) of a system (e.g. a plant or ecosystem) within a prescribed volume V is given by (e.g. Dewar 2003)

$$\sigma_{\text{chem}} = \int_V \left\{ \sum_i F_i \cdot \nabla \left(\frac{-\mu_i}{T} \right) - \sum_{i,r} \frac{\mu_i}{T} v_{ir} \mathcal{J}_r \right\} dV, \quad (2.1)$$

where F_i (a vector) is the molar flux density ($\text{mol m}^{-2}\text{s}^{-1}$) of chemical species i , μ_i (J mol^{-1}) is the chemical potential of species i , T (K) is the temperature, v_{ir} is the stoichiometric coefficient of species i in reaction r (positive for products and negative for reactants) and \mathcal{J}_r ($\text{mol m}^{-3}\text{s}^{-1}$) is the rate of reaction r per unit volume. In general, F_i , μ_i , T and \mathcal{J}_r are functions of space and time. The first term in curly brackets is the local rate of entropy production due to mass flow across chemical gradients (i.e. gradients in $-\mu_i/T$); the second term is the local rate of entropy production due to chemical reactions.

The local mass balance of chemical species i is described by the continuity equation

$$\frac{\partial \rho_i}{\partial t} = -\nabla \cdot F_i + \sum_r v_{ir} \mathcal{J}_r, \quad (2.2)$$

where ρ_i (mol m^{-3}) is the molar density. When the system is in a steady state ($\partial \rho_i / \partial t = 0$), equation (2.2) gives $\nabla \cdot F_i = \sum_r v_{ir} \mathcal{J}_r$ and equation (2.1) then simplifies to

$$\sigma_{\text{chem}} = - \int_{\Omega} \sum_i \frac{\mu_i}{T} F_i \cdot dS, \quad (2.3)$$

where Ω is the system boundary, and dS is the local surface element (a vector of magnitude $|dS|$ pointing in the direction outwardly normal to the surface). Equation (2.3) only involves contributions from species i whose mass flux across the boundary (F_i) is non-zero, and σ_{chem} may be interpreted as the rate of entropy export by those boundary fluxes.

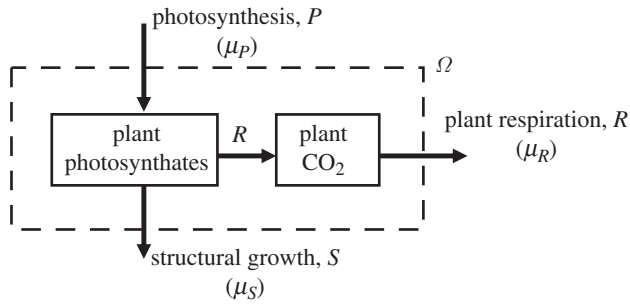


Figure 1. Carbon balance of plant photosynthates (CH_2O) and CO_2 . The dashed box indicates the system boundary Ω . The internal distributions of CH_2O and CO_2 within Ω are not represented. Plant structural biomass (protein, cellulose, etc.) lies outside Ω . The direction of the arrows indicates the sense in which fluxes are taken to be positive: P , photosynthesis; R , respiration for plant maintenance and growth; S , conversion of photosynthate carbon to new plant structure. Values of chemical potentials refer to the boundary Ω : μ_P , chemical potential of source photosynthate; μ_S , chemical potential of photosynthate at the sites of growth (sinks); μ_R , chemical potential of respired CO_2 . In the steady state, $R = P - S$.

In §3, I focus on the chemical entropy export from plants and ecosystems associated with three carbon species—photosynthates (sugars), carbon dioxide (CO_2) and structural biomass (proteins, cellulose, etc.). I ignore other potential contributions to σ_{chem} in plants (e.g. due to radiative exchange, plant water transport, evaporation of liquid water, etc.). I consider the maximization of σ_{chem} on different time scales. At each time scale, I identify a system of ‘fast’ carbon pools that can be considered to be in an approximate steady state on that time scale, i.e. the net carbon exchange between the ‘fast’ system and its environment is approximately zero. This approximation is useful because then σ_{chem} can be approximated by equation (2.3) in which Ω is the boundary of the ‘fast’ system. I will assume for simplicity that T is a constant in equation (2.3) (isothermal boundary conditions).

3. MAXIMUM CHEMICAL ENTROPY PRODUCTION AT DIFFERENT SCALES

(a) **MEP applied to plant photosynthates and CO_2** Figure 1 schematically depicts the carbon balance of plant photosynthates (CH_2O) and CO_2 . This system may be considered to be in an approximate steady state on a time scale of the order of 1 year (i.e. approximately zero net annual accumulation of CH_2O and CO_2).

The input flux is identified with the end products of photosynthesis (P). Some of the photosynthate is converted to CO_2 during plant respiration (R) and exported to the environment; the remainder is incorporated into various carbon products (proteins, cellulose, etc.) during structural growth (S). For each carbon flux across the system boundary, the chemical potential of the associated carbon species is indicated: μ_P , chemical potential of source photosynthate; μ_S , chemical potential of photosynthate at the sites of growth (sinks); μ_R , chemical potential of respired CO_2 .

Applying equation (2.3) (noting the minus sign) to the system in figure 1 (noting the flux sign convention) gives

$$\sigma_{\text{CH}_2\text{O}+\text{CO}_2} = \frac{1}{T} (P\mu_P - S\mu_S - R\mu_R). \quad (3.1)$$

Substituting the steady-state flux relation $R = P - S$ into equation (3.1) then gives

$$\sigma_{\text{CH}_2\text{O}+\text{CO}_2} = \frac{1}{T} \{P(\mu_P - \mu_R) - S(\mu_S - \mu_R)\}. \quad (3.2)$$

If one assumes that photosynthate is an ideal solute, then $\mu_P = \mu_{\text{ref}} + R_G T \ln(\rho_P/\rho_{\text{ref}})$ and $\mu_S = \mu_{\text{ref}} + R_G T \ln(\rho_S/\rho_{\text{ref}})$, where R_G is the universal gas constant, ρ_P and ρ_S are the source and sink photosynthate concentrations, and μ_{ref} and ρ_{ref} are the chemical potential and concentration of photosynthate in some reference state. Similarly, for CO_2 one may assume $\mu_R = \mu_{R,\text{ref}} + R_G T \ln(\rho_R/\rho_{R,\text{ref}})$. The chemical potentials μ_P , μ_S and μ_R will vary in time to some degree due to variations in ρ_P , ρ_S and ρ_R (which depend on the fluxes P , S and R). As a first approximation, I will ignore these variations and treat μ_P , μ_S and μ_R as fixed parameters. Then, from equation (3.2) and recalling that T is also assumed to be constant, we have

$$\sigma_{\text{CH}_2\text{O}+\text{CO}_2} \propto P - \lambda_C S, \quad (3.3)$$

where

$$\lambda_C = \frac{\mu_S - \mu_R}{\mu_P - \mu_R} \quad (3.4)$$

is a constant. According to the Münch hypothesis of phloem transport (e.g. Christy & Ferrier 1973), the internal movement of photosynthates between sources and sinks—represented, respectively, by the upper and lower system boundaries in figure 1—occurs from high to low concentrations (i.e. $\rho_P \geq \rho_S$), implying $\mu_P \geq \mu_S$. Also, we have $\mu_S \geq \mu_R$ since respiration involves the dissipation of high-quality substrates (CH_2O) to low-quality products (CO_2). Therefore, $\mu_P \geq \mu_S \geq \mu_R$ and so, from equation (3.4), $0 \leq \lambda_C \leq 1$. Note that the second law of thermodynamics ($\sigma_{\text{CH}_2\text{O}+\text{CO}_2} \geq 0$) is satisfied so long as $R \geq 0$ (since $R = P - S \geq 0$ and $\lambda_C \leq 1$ imply $P \geq S \geq \lambda_C S$).

When $\lambda_C = 0$, equation (3.3) implies that MEP is equivalent to maximizing P , which is a realistic goal from the perspective of natural selection; however, this lower limit is physiologically and thermodynamically unrealistic ($\mu_S = \mu_R$). The upper limit $\lambda_C = 1$ (i.e. $\mu_P = \mu_S$) is possibly a reasonable approximation for small plants (small internal gradients in CH_2O concentration). In this case, MEP is equivalent to maximizing plant respiration, $R = P - S$. At first sight, maximizing R might seem a less obvious goal for plant survival than maximizing P because R is often viewed negatively (especially by modellers) as a carbon ‘cost’ for plant growth (since $S = P - R$). This view neglects the fact that R drives all the metabolic processes that are crucial to plant function and survival (including growth, S) so that maximizing R is reasonable on fitness grounds. Moreover, in the steady state, maximizing R ($= P - S$) cannot be

sustained without also maximizing P , because photosynthesis provides the substrate for respiration. Consideration of the hypothetical limiting cases $\lambda_C = 0$ and $\lambda_C = 1$ therefore suggests that, across the entire range $0 \leq \lambda_C \leq 1$, maximization of $\sigma_{\text{CH}_2\text{O} + \text{CO}_2}$ (equation (3.3)) is reasonable from the perspective of natural selection.

To explore this suggestion in more detail, I now consider the biological implications of maximizing $\sigma_{\text{CH}_2\text{O} + \text{CO}_2} \propto P - \lambda_C S$ for the more realistic intermediate values $0 < \lambda_C < 1$. In general, P is a saturating function of plant light absorption (I) and plant nitrogen content (N) (e.g. Dewar 1996), while S is more nearly proportional to N (e.g. Ågren & Franklin 2003). It follows that there is an optimal value of N which maximizes $P - \lambda_C S$; as N increases, the 'benefit' of increased P is eventually offset by the 'cost' of increased $\lambda_C S$. It should be remembered, however, that the benefit and cost here are being interpreted in terms of chemical entropy production (=entropy export) rather than carbon gain.

As a simple example, let us assume the rectangular hyperbolic relationship $P = h\alpha kN/(\alpha I + kN)$ (Dewar 1996) and the linear relationship $S = gN$ (I , plant light absorption; N , plant nitrogen content; h , day-length; α , quantum yield; k , carboxylation coefficient; g , nitrogen growth efficiency). Maximization of $P - \lambda_C S$ then predicts that the optimal plant nitrogen content is

$$N_{\text{MEP}} = \frac{\alpha I \theta}{k}, \quad (3.5)$$

where $\theta = \sqrt{hk/\lambda_C g} - 1$. The optimal rate of structural growth is then predicted to be directly proportional to plant light interception, $S_{\text{MEP}} = \varepsilon_S I$, where $\varepsilon_S = \alpha g \theta / k$ can be interpreted as the plant growth 'light-use efficiency'. A linear relationship between plant growth rate and light absorption has been observed empirically over a wide range of different plant types (e.g. Dewar 1996 and references therein). The above equations imply that a similar result also applies to photosynthesis itself: $P_{\text{MEP}} = \varepsilon_P I$, where $\varepsilon_P = \alpha h \theta / (1 + \theta)$ is the photosynthetic light-use efficiency—I will use this result in §3b.

The nitrogen-based trade-off here between P and S is mathematically equivalent to the nitrogen-based trade-off between P and maintenance respiration proposed previously under the assumption that plants maximize their net primary productivity (Dewar 1996; Haxeltine & Prentice 1996). Only a verbal justification for that assumption was given—it seems reasonable for plant survival. Here, this trade-off is given a novel thermodynamic interpretation—it is the result of MEP applied to plant photosynthates and CO_2 .

(b) MEP applied to whole plants

Figure 2 depicts the carbon balance of whole plants. Here, the system boundary (Ω) in figure 1 has been extended to include plant structure. This extended system may be considered to be in an approximate steady state on a time scale of 1–10 years (i.e. of the order of the lifetime of plant structural biomass,

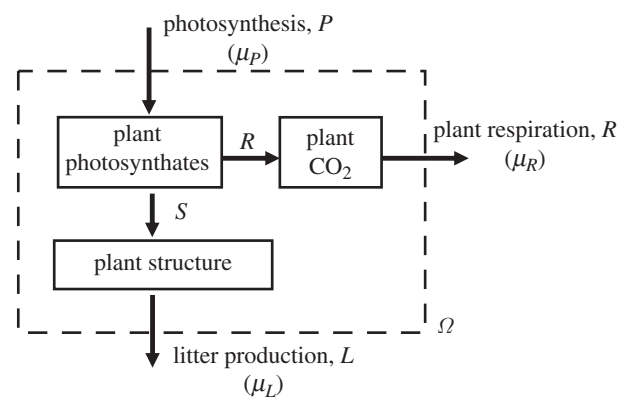


Figure 2. Whole-plant carbon balance. Notation as in figure 1, except that the system boundary (Ω) has been extended to include plant structure (proteins, cellulose, etc.). L , plant litter production; μ_L , chemical potential of plant litter. In the steady state, $R = P - L$.

which depends on plant type). Structural growth S is now an internal flux; litter production (L) takes the place of S as an external flux, and the associated chemical potential is μ_L .

Analogous to equation (3.1), the plant entropy export rate is given by

$$\sigma_{\text{plant}} = \frac{1}{T} (P\mu_P - L\mu_L - R\mu_R). \quad (3.6)$$

Substituting the steady-state flux relation $R = P - L$ into equation (3.6) then gives a result analogous to equation (3.3)

$$\sigma_{\text{plant}} \propto P - \lambda_P L, \quad (3.7)$$

where

$$\lambda_P = \frac{\mu_L - \mu_R}{\mu_P - \mu_R}. \quad (3.8)$$

Here, again, I have ignored variations in the chemical potentials μ_P , μ_L and μ_R , and the temperature T . As before, I assume that $\mu_P \geq \mu_R$ ($\text{CH}_2\text{O} \rightarrow \text{CO}_2$ representing dissipation of chemical free energy), and also $\mu_L \geq \mu_P$ (plant structure being more reduced than sugars), so that $\lambda_P \geq 1$. Then, the second law of thermodynamics ($\sigma_{\text{plant}} \geq 0$) is satisfied so long as $R \geq (\lambda_P - 1)L$ (since $R = P - L \geq (\lambda_P - 1)L$ implies $P \geq \lambda_P L$); this condition reflects the fact that structural growth is an active process (i.e. $\mu_L \geq \mu_P$) that is driven by the free energy generated by respiration (in the form of non-equilibrium ATP/ADP and NADPH/NADP ratios).

The chemical potentials μ_P and μ_R may be modelled as before in terms of the respective concentrations of CH_2O and CO_2 on the system boundary Ω . The chemical potential of litter (μ_L) is well defined theoretically as a function of its chemical composition by $\mu_L = \sum_k v_k \mu_k$ (v_k and μ_k being, respectively, the fraction and chemical potential of component k). However, the practical determination of μ_L remains challenging due to the compositional complexity of biomass (e.g. Meysman & Bruers 2007 and references therein); for the purposes of this study, I simply assume that μ_L is a given constant.

I now consider a simple example of the application of MEP to equation (3.7), which leads to the prediction of an optimal leaf biomass B_l . We have already seen from the maximization of $\sigma_{\text{CH}_2\text{O}+\text{CO}_2}$ on shorter time scales (§3a) that plant photosynthesis at the optimal nitrogen content is given by $P = \varepsilon_P I$, where ε_P is the photosynthetic light-use efficiency and I is plant light absorption. In general, I is a saturating function of B_l due to the effect of leaf mutual shading; a simple model of this is given by the Beer–Lambert law $I = I_{\text{in}}(1 - e^{-ksB_l})$, where I_{in} is the incident radiation at the top of the canopy, s is the leaf area per unit leaf biomass (inversely related to leaf thickness) and k (a function of leaf orientation and clumping) describes the exponential extinction of light within the canopy. In contrast, plant litter production L is more appropriately modelled as a linear function of each biomass compartment, $L = \sum_j m_j B_j$, where m_j is the specific mortality rate of biomass compartment j .

With reference to equation (3.7), as B_l increases (all other B_j being held fixed), the entropic ‘benefit’ of increased P (via increased light absorption I) is eventually offset by the entropic ‘cost’ of increased $\lambda_P L$. The optimal leaf biomass that maximizes σ_{plant} is easily calculated as

$$B_{l,\text{MEP}} = \frac{1}{ks} \ln \left(\frac{\varepsilon_P I_{\text{in}} ks}{\lambda_P m_l} \right). \quad (3.9)$$

The optimal rate of photosynthesis is then found to be $P_{\text{MEP}} = \varepsilon_P I_{\text{in}} - \lambda_P m_l / ks$.

The interpretation of observed leaf biomass in terms of an optimal trade-off between canopy photosynthesis and leaf litter production has been proposed previously (e.g. [McMurtrie 1985](#) and references therein). The objective function given by equation (3.7) is also mathematically similar to that adopted by [Franklin \(2007\)](#). In either case, only a verbal justification for the choice of objective function was given. Here, the use of equation (3.7) as an objective function for plant optimization models is given a new thermodynamic interpretation—it is the result of MEP applied at the whole-plant scale.

(c) MEP applied to ecosystems

Figure 3 depicts the carbon balance of an ecosystem. At this scale, the system boundary now includes litter and soil organic carbon. This system may be considered to be in an approximate steady state on a time scale of the order of 10–100 years (i.e. the residence time of carbon in litter and soil organic matter).

The ecosystem entropy export rate is (notation as in figure 3)

$$\sigma_{\text{ecosystem}} = \frac{1}{T} (P\mu_P - R_A\mu_R - R_H\mu_R). \quad (3.10)$$

Substituting the steady-state flux relation $R_A + R_H = P$ into equation (3.10) then yields (cf. equations (3.3) and (3.7))

$$\sigma_{\text{ecosystem}} \propto P(\mu_P - \mu_R) \propto P, \quad (3.11)$$

where again I have assumed that μ_P , μ_R and T are fixed. At the ecosystem scale, therefore, the

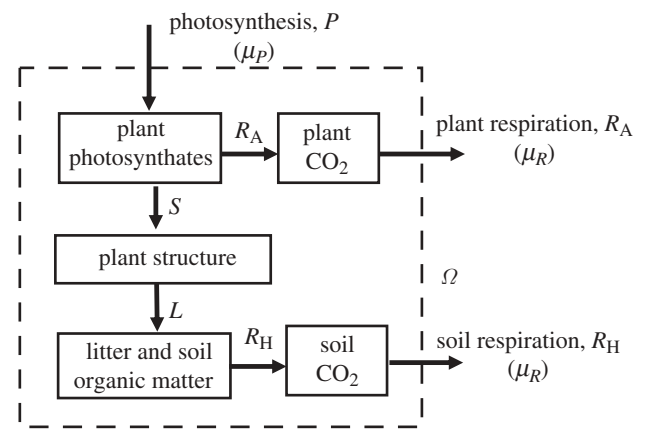


Figure 3. Ecosystem carbon balance. Notation as in figure 2, except that the system boundary (Ω) has been extended to include litter and soil organic matter. R_A , autotrophic (plant) respiration; R_H , heterotrophic (soil) respiration. In the steady state, $R_A + R_H = P$.

steady-state chemical entropy export is associated with the overall dissipative reaction that converts photosynthates (CH_2O) to CO_2 ($\mu_P \geq \mu_R$), the second law ($\sigma_{\text{ecosystem}} \geq 0$) is automatically satisfied since $P \geq 0$ and MEP is equivalent to maximizing canopy photosynthesis. Maximization of canopy photosynthesis has been proposed previously as a plant optimization goal (e.g. [Field 1983](#); [Anten 2005](#); [McMurtrie et al. 2008](#)). MEP provides a thermodynamic justification for maximizing P —it is the result of MEP applied at the ecosystem scale.

The application of optimization theories is traditionally confined to the plant or canopy scales, reflecting the popular view that natural selection acts uniquely at the level of individual organisms. But as the analysis here suggests, MEP provides an alternative thermodynamic interpretation of optimization theories that can be extended beyond individual plants to whole ecosystems.

As a simple example of applying MEP at this scale, recall the result $P_{\text{MEP}} = \varepsilon_P I_{\text{in}} - \lambda_P m_l / ks$ obtained previously by maximizing whole-plant entropy export (§3b). The maximization of P may thus be accomplished in part by maximizing $\varepsilon_P I_{\text{in}}$. [Kleidon \(2004\)](#) has demonstrated that a maximum in $\varepsilon_P I_{\text{in}}$ exists with respect to variations in stomatal conductance, when large-scale vegetation–atmosphere feedbacks are taken into account. Specifically, increasing stomatal conductance leads, on the one hand, to increased plant CO_2 uptake (hence increased ε_P) and, on the other hand, to increased transpiration (hence increased cloud cover and reduced I_{in} at the land surface). Optimization of stomatal conductance was found to predict realistic vegetation–climate states ([Kleidon 2004](#)).

We may envisage MEP (maximum $P_{\text{MEP}} = \varepsilon_P I_{\text{in}} - \lambda_P m_l / ks$) also operating through minimization of the term $\lambda_P m_l / ks$, involving co-adaptation of leaf lifespan (affecting m_l), leaf orientation (affecting k) and leaf thickness (affecting s). Observed correlations between leaf traits (e.g. [Reich et al. 1992](#); [Wright et al. 2004](#)) offer a fertile testing ground for MEP and other

candidate optimization theories of plant function (e.g. [McMurtrie & Dewar submitted](#)). Finally, extending MEP to ecosystems also raises the possibility of predicting optimal soil characteristics (e.g. soil depth, moisture content and nutrient cycling), since the long-term maximization of photosynthesis may involve trade-offs that depend on plant–soil feedbacks.

4. CONCLUSIONS

Within well-defined approximations (fixed chemical potentials and fixed temperature), MEP is closely related to various plant optimization theories that have been proposed previously on the basis of ad hoc measures of individual fitness. Like traditional plant optimization theories, MEP can predict optimal plant behaviour that is reasonable from the perspective of natural selection. The different objective functions of these theories emerge as examples of entropy production on different spatio-temporal scales. Moreover, as a system-level thermodynamic principle, MEP extends the traditional optimization approach beyond individual plants to vegetation canopies and whole ecosystems. This suggests that MEP offers a unifying optimization principle for plant and ecosystem function, and that entropy production might be considered as a general objective function for biological systems (e.g. [Dewar *et al.* 2006](#); [Meysman & Bruers 2007](#)).

Further work is needed to determine whether MEP improves on previous optimization theories in predicting observed plant function. To this end, the simple analysis presented here for illustrative purposes might be developed further to include variable chemical potentials (e.g. [Meysman & Bruers 2007](#)). An outstanding practical issue here is how to estimate the chemical potential of plant litter (μ_L) required when applying MEP at the whole-plant scale ([figure 2](#)). Also, the simple applications of MEP presented in §3 do not incorporate resource supply constraints such as nitrogen and water availability. Some recent plant optimization models incorporating resource supply constraints are reviewed in [Dewar *et al.* \(2009\)](#), see also [McMurtrie & Dewar \(submitted\)](#). These constraints might also be introduced into the MEP framework presented here.

Conceptually, MEP offers a radically new perspective on the adaptive behaviour and evolution of plants. The proposed statistical explanation of MEP—a subject of open debate ([Dewar 2003, 2005, 2009](#); [Martyushev & Seleznev 2006](#); [Bruers 2007](#); [Grinstein & Linsker 2007](#); [Niven 2009](#))—is that the MEP state is selected by nature because it can be realized microscopically in an overwhelmingly greater number of ways than any other non-equilibrium state. MEP therefore suggests a new and extended paradigm for biological evolution—survival of the likeliest ([Whitfield 2007](#))—which applies at scales ranging from biomacromolecules to ecosystems (e.g. [Dewar *et al.* 2006](#); [Dewar & Porté 2008](#)), not just to individual organisms, and which encompasses both living and non-living structures.

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REFERENCES

- Ackerly, D. D. 1999 Self-shading, carbon gain and leaf dynamics: a test of alternative optimality models. *Oecologia* **119**, 300–310. (doi:10.1007/s004420050790)
- Ågren, G. I. & Franklin, O. 2003 Root : shoot ratios, optimization and nitrogen productivity. *Ann. Bot.* **92**, 795–800. (doi:10.1093/aob/mcg203)
- Anten, N. P. R. 2005 Optimal photosynthetic characteristics of individual plants in vegetation stands and implications for species coexistence. *Ann. Bot.* **95**, 495–506. (doi:10.1093/aob/mci048)
- Bruers, S. 2007 A discussion on maximum entropy production and information theory. *J. Phys. A* **40**, 7441–7450. (doi:10.1088/1751-8113/40/27/003)
- Christy, A. L. & Ferrier, J. M. 1973 A mathematical treatment of Munch's pressure-flow hypothesis of phloem translocation. *Plant Physiol.* **52**, 531–538. (doi:10.1104/pp.52.6.531)
- Cowan, I. R. & Farquhar, G. D. 1977 Stomatal function in relation to leaf metabolism and environment. *Soc. Exp. Biol. Symp.* **31**, 471–505.
- Cramer, W. *et al.* 2001 Global responses of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biol.* **7**, 357–373. (doi:10.1046/j.1365-2486.2001.00383.x)
- Dewar, R. C. 1996 The correlation between plant growth and intercepted radiation: an interpretation in terms of optimal plant nitrogen content. *Ann. Bot.* **78**, 125–136. (doi:10.1006/anbo.1996.0104)
- Dewar, R. C. 2003 Information theory explanation of the fluctuation theorem, maximum entropy production and self-organized criticality in non-equilibrium stationary states. *J. Phys. A* **36**, 631–641. (doi:10.1088/0305-4470/36/3/303)
- Dewar, R. C. 2004 Maximum entropy production and non-equilibrium statistical mechanics. In *Non-equilibrium thermodynamics and entropy production: life, earth and beyond* (eds A. Kleidon & R. Lorenz), pp. 41–55. Heidelberg, Germany: Springer Publishers.
- Dewar, R. C. 2005 Maximum entropy production and the fluctuation theorem. *J. Phys. A* **38**, L371–L381. (doi:10.1088/0305-4470/38/21/L01)
- Dewar, R. C. 2009 Maximum entropy production as an algorithm that translates physical assumptions into macroscopic predictions: don't shoot the messenger. *Entropy* (Special Issue. *What is maximum entropy production and how should we apply it?*) **11**, 931–944. (doi:10.3390/e11040931)
- Dewar, R. C. & Porté, A. 2008 Statistical mechanics unifies different ecological patterns. *J. Theor. Biol.* **251**, 389–403. (doi:10.1016/j.jtbi.2007.12.007)
- Dewar, R. C., Medlyn, B. E. & McMurtrie, R. E. 1998 A mechanistic analysis of light and carbon use efficiencies. *Plant Cell Environ.* **21**, 573–588. (doi:10.1046/j.1365-3040.1998.00311.x)
- Dewar, R. C., Juretić, D. & Županović, P. 2006 The functional design of the rotary enzyme ATP synthase is consistent with maximum entropy production. *Chem. Phys. Lett.* **430**, 177–182. (doi:10.1016/j.cplett.2006.08.095)

- Dewar, R. C., Franklin, O., Mäkelä, A., McMurtrie, R. E. & Valentine, H. T. 2009 Optimal function explains forest responses to global change. *BioScience* **59**, 127–139. (doi:10.1525/bio.2009.59.2.6)
- Field, C. B. 1983 Allocating leaf nitrogen for the maximization of carbon gain—leaf age as a control on the allocation program. *Oecologia* **56**, 341–347. (doi:10.1007/BF00379710)
- Franklin, O. 2007 Optimal nitrogen allocation controls tree responses to elevated CO₂. *New Phytol.* **174**, 811–822. (doi:10.1111/j.1469-8137.2007.02063.x)
- Franklin, O. & Ågren, G. I. 2002 Leaf senescence and resorption as mechanisms of maximising photosynthetic production during canopy development at N limitation. *Funct. Ecol.* **16**, 727–733. (doi:10.1046/j.1365-2435.2002.00674.x)
- Givnish, T. J. (ed.) 1986 *On the economy of plant form and function*. Cambridge, UK: Cambridge University Press.
- Grinstein, G. & Linsker, R. 2007 Comments on a derivation and an application of the 'maximum entropy production' principle. *J. Phys. A* **40**, 9717–9720. (doi:10.1088/1751-8113/40/31/N01)
- Haxeltine, A. & Prentice, I. C. 1996 A general model for the light use efficiency of primary production. *Funct. Ecol.* **10**, 551–561. (doi:10.2307/2390165)
- Hikosaka, K. 2003 Leaf canopy as a dynamic system: eco-physiology and optimality in leaf turnover. *Ann. Bot.* **95**, 521–533. (doi:10.1093/aob/mci050)
- Kleidon, A. 2004 Optimized stomatal conductance of vegetated land surfaces and its effect on simulated productivity and climate. *Geophys. Res. Lett.* **31**, L21203. (doi:10.1029/2004GL020769)
- Kull, O. 2002 Acclimation of photosynthesis in canopies: models and limitations. *Oecologia* **133**, 267–279. (doi:10.1007/s00442-002-1042-1)
- Levy, P. E., Wendler, R., Van Oijen, M., Cannell, M. G. R. & Millard, P. 2004 The effects of nitrogen enrichment on the carbon sink in coniferous forests: uncertainty and sensitivity analyses of three ecosystem models. *Wat. Air Soil Poll.: Focus* **4**, 67–74. (doi:10.1007/s11267-004-3015-3)
- Luo, Y. *et al.* 2008 Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biol.* **14**, 1986–1999. (doi:10.1111/j.1365-2486.2008.01629.x)
- Mäkelä, A. & Sievänen, R. 1992 Height growth strategies in open-grown trees. *J. Theor. Biol.* **159**, 443–467. (doi:10.1016/S0022-5193(05)80690-3)
- Mäkelä, A., Givnish, T. J., Berninger, F., Buckley, T. N., Farquhar, G. D. & Hari, P. 2002 Challenges and opportunities of the optimality approach in plant ecology. *Silv. Fenn.* **36**, 605–614.
- Mäkelä, A., Valentine, H. & Helmisaari, S. 2008 Optimal co-allocation of carbon and nitrogen in a closed forest stand at steady state. *New Phytol.* **180**, 114–123. (doi:10.1111/j.1469-8137.2008.02558.x)
- Martyushev, L. M. & Seleznev, V. D. 2006 Maximum entropy production principle in physics, chemistry and biology. *Phys. Rep.* **426**, 1–45. (doi:10.1016/j.physrep.2005.12.001)
- McMurtrie, R. E. 1985 Forest productivity in relation to carbon partitioning and nutrient cycling: a mathematical model. In *Attributes of trees as crop plants* (eds M. G. R. Cannell & J. E. Jackson), pp. 194–207. Huntingdon, UK: Institute of Terrestrial Ecology.
- McMurtrie, R. E. & Dewar, R. C. Submitted. Leaf trait variations explained by the hypothesis that plants maximise their canopy carbon export over the lifespan of leaves. *Proc. Natl Acad. Sci. USA*.
- McMurtrie, R. E., Norby, R. J., Medlyn, B. E., Dewar, R. C., Pepper, D. A., Reich, P. B. & Barton, C. V. M. 2008 Why is plant-growth response to elevated CO₂ amplified when water is limiting, but reduced when nitrogen is limiting? A growth optimisation hypothesis. *Funct. Biol.* **35**, 521–534. (doi:10.1071/FP08128)
- Meysman, F. J. R. & Bruers, S. 2007 A thermodynamic perspective on food webs: quantifying entropy production within detrital-based ecosystems. *J. Theor. Biol.* **249**, 124–139. (doi:10.1016/j.jtbi.2007.07.015)
- Niven, R. K. 2009 Steady state of a dissipative flow-controlled system and the maximum entropy production principle. *Phys. Rev. E* **80**, 021113. (doi:10.1103/PhysRevE.80.021113)
- Reich, P. B., Walters, M. B. & Ellsworth, D. S. 1992 Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol. Monogr.* **62**, 365–392. (doi:10.2307/2937116)
- Reynolds, J. F. & Thornley, J. H. M. 1982 A shoot : root partitioning model. *Ann. Bot.* **49**, 585–597.
- Schymanski, S. J., Sivapalan, M., Roderick, M. L., Hutley, L. B. & Beringer, J. 2009 An optimality-based model of the dynamic feedbacks between natural vegetation and the water balance. *Wat. Resour. Res.* **45**, W01412. (doi:10.1029/2008WR006841)
- Wang, Y.-P., Leuning, R., Cleugh, H. A. & Coppin, P. A. 2001 Parameter estimation in surface exchange models using nonlinear inversion: how many parameters can we estimate and which measurements are most useful? *Global Change Biol.* **7**, 495–510. (doi:10.1046/j.1365-2486.2001.00434.x)
- Whitfield, J. 2005 Order out of chaos. *Nature* **436**, 905–907. (doi:10.1038/436905a)
- Whitfield, J. 2007 Survival of the likeliest? *PLoS (Biol)* **5**, e142. (doi:10.1371/journal.pbio.0050142)
- Wright, I. J. *et al.* 2004 The worldwide leaf economics spectrum. *Nature* **428**, 821–827. (doi:10.1038/nature02403)