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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 & Siievänen 1992) and leaf-area index (e.g. McMurtrie 1985; Franklin & Agren 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...
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; Hirooka 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 literature, 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.

The present viewpoint is that MEP is a statistical principle that addresses the statistical nature of evolution. The MEP hypothesis is that living systems are sustained by a constant rate of entropy production, which is a fundamental theorem of the second law of thermodynamics. This hypothesis is supported by a large body of empirical evidence, including studies of the evolution of biomacromolecules and the ecology of ecosystems.

2. CHEMICAL ENTROPY PRODUCTION BY PLANTS AND ECOSYSTEMS

The instantaneous rate of chemical entropy production in plants and ecosystems (\( \sigma_{chem} \)) is given by (e.g. Dewar 2003)

\[
\sigma_{chem} = \int_V \left\{ \sum_i F_i \cdot \nabla \left( \frac{-\mu_i}{T} \right) - \sum_{i,j} \frac{\mu_i}{T} v_{ij} J_{ij} \right\} dV,
\]

where \( F_i \) (a vector) is the molar flux density, \( \mu_i \) is the chemical potential of species \( i \), \( T \) is the temperature, \( v_{ij} \) is the stoichiometric coefficient of species \( i \) in reaction \( r \), and \( J_{ij} \) is the rate of reaction \( r \) per unit volume. In general, \( F_i, \mu_i \) and \( J_{ij} \) 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

\[
\frac{\partial \rho_i}{\partial t} = -\nabla \cdot F_i + \sum_r v_{ir} J_r,
\]

where \( \rho_i \) is the molar density. When the system is in a steady state (\( \partial \rho_i/\partial t = 0 \)), equation (2.2) gives

\[
\nabla \cdot F_i = \sum_r v_{ir} J_r,
\]

and equation (2.1) then simplifies to

\[
\sigma_{chem} = -\int_q \sum_i \frac{\mu_i}{T} F_i \cdot d\Omega,
\]

where \( \Omega \) is the system boundary, and \( d\Omega \) is the local surface element (a vector of magnitude \( |d\Omega| \) 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 \( \sigma_{chem} \) may be interpreted as the rate of entropy export by those boundary fluxes.
Figure 1. Carbon balance of plant photosynthates (CH$_2$O) and CO$_2$. The dashed box indicates the system boundary $\Omega$. The internal distributions of CH$_2$O and CO$_2$ within $\Omega$ are not represented. Plant structural mass (protein, cellulose, etc.) lies outside $\Omega$. 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 $\Omega$: $\mu_P$, chemical potential of source photosynthate; $\mu_S$, chemical potential of photosynthate at the sites of growth (sinks); $\mu_R$, chemical potential of respired CO$_2$. In the steady state, $P = R - S$.

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 $\sigma_{\text{chem}}$ in plants (e.g. due to radiative exchange, plant water transport, evaporation of liquid water, etc.). I consider the maximization of $\sigma_{\text{chem}}$ 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 $\sigma_{\text{chem}}$ can be approximated by equation (2.3) in which $\Omega$ 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$_2$O) 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$_2$O and CO$_2$).

The input flux is identified with the end products of photosynthesis ($P$). Some of the photosynthesize 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: $\mu_P$, chemical potential of source photosynthate; $\mu_S$, chemical potential of photosynthate at the sites of growth (sinks); $\mu_R$, 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

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

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

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

If one assumes that photosynthate is an ideal solute, then $\mu_P = \mu_{\text{chem}} + R_G T \ln(p_P/p_{\text{ref}})$ and $\mu_S = \mu_{\text{chem}} + R_G T \ln(p_S/p_{\text{ref}})$, where $R_G$ is the universal gas constant, $p_P$ and $p_S$ are the source and sink photosynthesize concentrations, and $p_{\text{chem}}$ are the chemical potential and concentration of photosynthesize in some reference state. Similarly, for CO$_2$ one may assume $\mu_R = \mu_{\text{chem}} + R_G T \ln(p_R/p_{\text{ref}})$. The chemical potentials $\mu_P$, $\mu_S$ and $\mu_R$ will vary in time to some degree due to variations in $p_P$, $p_S$ and $p_R$ (which depend on the fluxes $P$, $S$ and $R$). As a first approximation, I will ignore these variations and treat $\mu_P$, $\mu_S$ and $\mu_R$ as fixed parameters. Then, from equation (3.2) and recalling that $T$ is also assumed to be constant, we have

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

where

$$\lambda_C = \frac{\mu_S - \mu_R}{\mu_P - \mu_R}.$$

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. $p_P > p_S$), implying $\mu_P > \mu_S$. Also, we have $\mu_S > \mu_R$ since respiration involves the dissipation of high-quality substrates (CH$_2$O) to low-quality products (CO$_2$). Therefore, $\mu_P > \mu_S > \mu_R$ 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$_2$O 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 ($\equiv$ entropy export) rather than carbon gain.

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

$$N_{\text{MEP}} = \frac{\alpha I}{k},$$

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, $S_{\text{MEP}} = eS_I$, where $eS_I = \alpha g \theta/k$ 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: $P_{\text{MEP}} = eP_I$, where $eP_I = \alpha h \theta/(1 + \theta)$ is the photosynthetic light-use efficiency—$I$ will use this result in §36.

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 photosyntheses and CO$_2$.

(b) MEP applied to whole plants

Figure 2 depicts the carbon balance of whole plants. Here, the system boundary ($\Omega$) 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, 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 $\mu_L$.

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

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

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

$$\sigma_{\text{plant}} \propto P - \lambda_P L,$$

where

$$\lambda_P = \frac{\mu_L - \mu_R}{\mu_P - \mu_R}.$$  

Here, again, I have ignored variations in the chemical potentials $\mu_P$, $\mu_L$, and $\mu_R$ and the temperature $T$. As before, I assume that $\mu_P \geq \mu_R$ (CH$_2$O $- \text{CO}_2$ 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 $\mu_P$ and $\mu_R$ may be modelled as before in terms of the respective concentrations of CH$_2$O and CO$_2$ on the system boundary $\Omega$. The chemical potential of litter ($\mu_L$) is well defined theoretically as a function of its chemical composition by $\mu_L = \sum v_k \mu_k$ ($v_k$ and $\mu_k$ being, respectively, the fraction and chemical potential of component $k$). However, the practical determination of $\mu_L$ 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 $\mu_L$ is a given constant.

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

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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 $\alpha_{\text{CH}_2\text{O},\text{CO}_2}$ on shorter time scales (§3a) that plant photosynthesis at the optimal nitrogen content is given by $P = e_p I$, where $e_p$ 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 $I = I_m(1 - e^{-k_l B_l})$, where $I_m$ 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 and 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 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 $\alpha_{\text{plant}}$ is easily calculated as

$$B_{l,\text{MEP}} = \frac{1}{k_s} \ln \left( \frac{e_p I_m k_s}{\lambda_p m_l} \right).$$

(3.9)

The optimal rate of photosynthesis is then found to be $P_{\text{MEP}} = e_p I_m - \lambda_p m_l / k_s$.

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)

$$\alpha_{\text{ecosystem}} = \frac{1}{T} \{ P \mu_p - R_A \mu_R - R_H \mu_R \}. \tag{3.10}$$

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

$$\alpha_{\text{ecosystem}} \propto P(\mu_p - \mu_R) \propto P, \tag{3.11}$$

where again I have assumed that $\mu_p$, $\mu_R$ and $T$ are fixed. At the ecosystem scale, therefore, the steady-state chemical entropy export is associated with the overall dissipative reaction that converts photosynthates ($\text{CH}_2\text{O}$) to $\text{CO}_2$ ($\mu_p > \mu_R$), the second law ($\alpha_{\text{ecosystem}} \geq 0$) is automatically satisfied since $P > 0$ 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 $P_{\text{MEP}} = e_p I_m - \lambda_p m_l / k_s$ obtained previously by maximizing whole-plant entropy export (§3b). The maximization of $P$ may thus be accomplished in part by maximizing $e_p I_m$. Kleidon (2004) has demonstrated that a maximum in $e_p I_m$ 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 $\text{CO}_2$ uptake (hence increased $e_p$) and, on the other hand, to increased transpiration (hence increased cloud cover and reduced $I_m$ at the land surface). Optimization of stomatal conductance was found to predict realistic vegetation–climate states (Kleidon 2004).

We may envisage MEP (maximum $P_{\text{MEP}} = e_p I_m - \lambda_p m_l / k_s$) also operating through minimization of the term $\lambda p m_l / k_s$, 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 ($\mu_L$) 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, 2006; 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 like-liest (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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