

Fit, Fitter, Fittest; Where Does Optimisation Fit In?

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1 Introduction

Optimisation is about making something, generally a complex system of interacting elements, as fit as possible. The purpose for which it is to be made fit, and the constraints on the elements and interactions, are defined. It is altogether different when optimality considerations are used to shed light on the way in which natural organisms relate to their physical and biotic circumstances, and why it is that particular phenotypes correlate with particular environments. That is to engage in what has been termed reverse engineering: identification of the attributes of an organism that contribute to its being fit. The only satisfactory definition of the purpose of its fitness is survival.

Of course, the notion that the tautology of Spencer's phrase, 'Survival of the fittest', somehow undermines the concept of evolution by natural selection can be dismissed. And, in the context of this conference, it is unnecessary to consider the work of evolutionary geneticists who define fitness in terms of alleles conferring advantages in survival and propagation, and thus do what Dawkins (1992) describes as 'whatever it takes to make the survival of the fittest into a tautology'. But can fitness be defined in a way that is independent of survival? Dawkins has written about the 'original' use of the term.

'It did not have a precise technical meaning, and the fittest were not *defined* as those that survive. Fitness meant, roughly, the ability to survive and reproduce, but it was not defined and measured precisely synonymous with reproductive success. It had a range of specific meanings, depending on the particular aspect of life one was considering.' Dawkins provides some examples. 'If the subject of attention was efficiency in grinding vegetable food, the fittest individuals were those with the hardest teeth or the most powerful jaw muscles. In different contexts the fittest individuals would be taken to mean those with the keenest eyes, the strongest leg muscles, the sharpest ears, the swiftest reflexes. These capacities and abilities, along with countless others, were supposed to improve over the generations, and natural selection effected that improvement. Survival of the fittest was a general characterization of these particular improvements. There is nothing tautological about that.'

However, if the application of optimality theory is confined to particular attributes, or groups of attributes within an organism, it must be assumed that natural selection has had those particular attributes at its disposal, so to speak, and that all the other attributes impinging on them are fixed, much as though they were part of an unchanging abiotic environment. Most problems cannot be

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satisfactorily constricted in this way. For example, it is inadequate to discuss the ideal arrangement of foliage in relation to light interception without also taking into account the economy of the supporting structure, plasticity in the physical arrangement and enzymatic composition of the chloroplasts, implications for water use, and so on (Givnish 1988). Nor can the sequence of plant development be ignored. Fitness in shoot geometry and foliage display at any one stage of development will place constraints on fitness at both earlier and later stages. To encompass development in optimisation analysis is a daunting task. But if analysis is confined to a particular stage of development then the range of problems that can be usefully addressed is severely limited.

Also, there will be attributes that do not, or seem not to, contribute to fitness. Any species carries 'baggage' relating to its tortuous, and largely unknown, evolutionary history. Lewontin (1987), one of the sternest critics of optimality theory in biology, defines the difficulty that arises. 'If every deviation from the optimum we expect is assumed to be an historical accident, then optimality theory is vacuous. If we deny the importance of historical contingencies, it is patently false.' He remarks, 'Between these two it is not clear to me how much space is left for enlightenment.'

There is a related problem. Optimisation demands attention not only to what actually exists, but to what does not exist. Eddington, the astronomer, once remarked (Fisher 1958), 'No practical biologist interested in sexual reproduction would be led to work out the detailed consequences experienced by organisms having three or more sexes; yet what else should he do if he wishes to understand why the sexes are, in fact, always two?' We can immediately see an objection to this. There is the implicit assumption that if, in fact, the sexes are always two, it is only because the possession of three would confer no selective advantage. The 'practical' biologist might be inclined to assume, not that a stable coexistence of three sexes in a higher species is impossible in principle, but that it is attainable only by one of innumerable paths evolution has happened not to take (but see Hurst and Hamilton 1992).

The difficulty is avoided if attention is confined only to what is observed to exist. This is what is done in attempting to explain why one

phenotype, rather than others, is successful in a particular environment. It is a rather restricted form of optimisation. To show that the alternatives are less fit, demonstrates only that the one phenotype is least unfit, not that it is optimal in any absolute sense.

Finally, the conclusion of any optimisation analysis in biology is not a design, but a theory. Therefore it must be testable. It is not sufficient that it provide a plausible explanation as to why observed attributes are as they are. It must have something to say about attributes not yet observed also. Of course, there should be some latitude given to hypotheses that are at first light merely plausible. If a strictly Popperian attitude to the theory of natural selection had been applied (as indeed many wished), Darwinism would hardly have survived into the twentieth century.

In what follows an attempt will be made to illustrate some of these matters. The examples are not new and are not chosen as especially appropriate to the purpose; they merely happen to be those that this contributor has thought most about.

2 Partitioning of Nitrogen between Two Enzymes

The essence of autotrophy in green plants is photosynthesis and one of the limitations to rate of photosynthesis is the amount of nitrogen available for the synthesis of the various enzymes involved. Let us consider the function of two particular enzymes. Ribulose-bisphosphate carboxylase/oxygenase, which accounts for some 50% of leaf protein, catalyses the first step in the chemical fixation of carbon in C₃ plants. Carbonic anhydrase comprises no more than 3% of leaf protein, but enhances, so it has been suggested, the activity of carboxylase through a process which Enns (1967) termed facilitated diffusion.

Although carbon dioxide enters the chloroplast as a gas in solution and is fixed in the unhydrated form, transport within the chloroplast is not confined to the diffusion of CO₂ per se. There is a second pathway which may be expressed, hydration ⇒ diffusion of bicarbonate ⇒ dehydration. As the equilibrium concentration of bicarbonate is some fifty times greater than that of CO₂, and

the effective diffusion coefficient of bicarbonate is probably not very much less (even allowing for impedance by thylakoid membranes) than that of CO_2 , there is considerable scope for this path to enhance the overall ease of transport. But it requires the presence of carbonic anhydrase to catalyse the hydration:dehydration processes which would otherwise be far too slow. How much anhydrase relative to carboxylase 'should' there be, for any given investment of nitrogen in the two enzymes?

The procedure is to find the form of the function

$$A = A(N_a, N_c, \dots) \quad (1)$$

A being rate of CO_2 assimilation, and N_a and N_c the corresponding amounts of anhydrase and carboxylase, respectively, as represented by the amounts of nitrogen they incorporate. Obviously the solution also involves the kinetic properties of the two enzymes and parameters such as diffusion coefficients, chloroplast dimensions, and intercellular partial pressure of CO_2 . The mathematics, and the appropriate values of the parameters have been discussed elsewhere (Cowan 1986).

Fig. 1 shows estimates of the influence of carbonic anhydrase on carbon assimilation. The upper curve relates to a particular constant concentration of carboxylase. It is one of diminishing returns, but suggests there cannot be too much of a good thing. The lower curve assumes there is only a certain amount of nitrogen, $N = N_a + N_c$, available for the synthesis of carboxylase and anhydrase. Therefore one molecule of carboxylase must be sacrificed for each additional three of anhydrase, because the molecular weight of the former is three times that of the latter. There is now a maximum rate of assimilation corresponding to

$$(\partial A / \partial N_a)_N = 0 \quad (2)$$

It occurs at $N_a = 2.7$ mol anhydrase per mol of chlorophyll. Assays of carbonic anhydrase activity in 13 dicotyledonous species (Atkins et al. 1972 a,b) convert to 2.3 ± 1.5 mol per mol chlorophyll.

This apparently satisfactory agreement can be tested in more detail. Analysis indicates that the

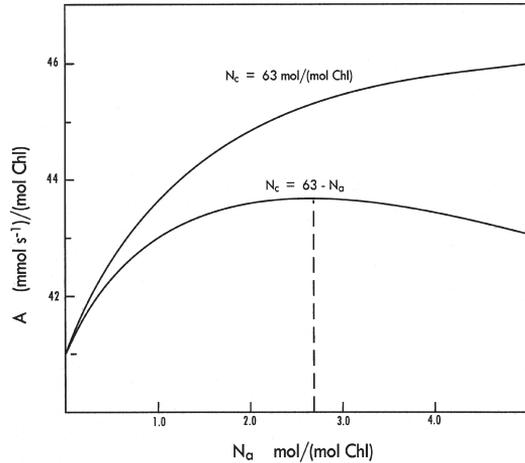


Fig. 1. Net rate of CO_2 fixation in a chloroplast, A , as a function of the amount of nitrogen incorporated in carbonic anhydrase, N_a . The uppermost curve assumes the amount of nitrogen incorporated in ribulose-biphosphate carboxylase, N_c , is constant; the other that $N_c + N_a$ is constant. Intercellular partial pressure of CO_2 is taken to be $230 \mu\text{bar}$, and the thickness of the chloroplast as $1.7 \mu\text{m}$. From Cowan (1986).

optimal amount of carbonic anhydrase is rather insensitive to the assumed intercellular pressure of CO_2 , but varies with amount of carboxylase and size of chloroplast, both of which differ amongst species and with conditions of growth. The results of further investigation have yet to be published. However the purpose of this article is not to sustain the validity of any particular optimisation hypothesis in detail, but to make general remarks about the nature and potential usefulness of various hypotheses. In this instance three comments seem worthwhile.

First, the hypothesis is falsifiable. It does not simply offer a possible explanation of what has already been observed; it predicts relationships not previously investigated, but which are susceptible to investigation.

Second, insofar as it turns out to be valid, it provides information about plant metabolism that is not easily achieved in any other way. The function of anhydrase in chloroplasts can, in principle, be tested empirically, for it has nothing to do with

optimisation theory. It is necessary to inhibit, by chemical or genetic means, the activity of carbonic anhydrase in chloroplasts, and compare rate of carbon fixation with that in untreated chloroplasts. However, such tests are probably insufficiently sensitive, given that it is predicted inhibition would decrease rate of carbon fixation by no more than a few percent (Badger and Pearce 1994).

Finally, we may note that we have dealt with two hypotheses, not one. Strictly one should perhaps argue that neither is proven; all that can be said is, *if* nitrogen is optimally shared between the two enzymes then the role of anhydrase is facilitated diffusion, and *if* the role of anhydrase is facilitated diffusion then nitrogen is optimally shared between the two enzymes. However, if neither hypothesis were valid, it is exceedingly unlikely that the amount of anhydrase would be consistent with the validity of both. Therefore the evidence weighs in favour of both hypotheses.

3 Marginal Efficiency of Nitrogen

The foregoing analysis is particularly simple in that carboxylase and anhydrase work in tandem, their activities affecting rate of assimilation only when the photosynthetic system is light-saturated. (It can be assumed that the reduction of photorespiration due to facilitated diffusion is very small at other times). The optimal division of nitrogen investment between the enzymes of the 'dark' reaction and those of the 'light' reactions is more complex, because it involves temporal variation in irradiance (Evans 1988). Still more so is the spatial distribution of photosynthetic activity per unit area of leaf within the foliage of an entire plant (Field 1988). A somewhat simplistic framework encompassing such matters is as follows.

Let A_T be the amount of carbon fixed by the entire foliage of a plant during a 'typical' day, and N_a be redefined as the amount of nitrogen in *any*, or all, of the enzymes involved in carbon fixation in *any* of the elements of the foliage – chloroplast, cell, leaf, or leaf layer. N_c will be taken to be its *complement*, that is to say $N_c = N - N_a$ with N now being the total amount of nitrogen invested in

enzymes associated with carbon fixation. Efficient allocation of nitrogen demands that

$$A_T(N_a, N_c) - \mu \cdot N \text{ is a maximum} \quad (3)$$

in which μ is an undetermined multiplier. Differentiating we have

$$(\partial A_T / \partial N_a)_{N_c} = (\partial A_T / \partial N_c)_{N_a} = dA_T / dN = \mu \quad (4)$$

The multiplier μ is, in economic terms, a marginal efficiency of investment. Provided the $A_T(N)$ curve is convex, as we can be confident is the case, it defines the point beyond which the worth of any putative further investment in N exceeds the value of its return in terms of A_T .

Because

$$(\partial A_T / \partial N_a)_N = (\partial A_T / \partial N_a)_{N_c} - (\partial A_T / \partial N_c)_{N_a}$$

it follows that

$$(\partial A_T / \partial N_a)_N = 0 \quad (5)$$

which is a generalised form of Eq. 2.

The inadequacies of this paradigm are evident; it does not take account of the longevity of leaves, the build-up of photosynthetic activity in growing leaves, the conversion of young 'sun' leaves to old 'shade' leaves as a plant develops, or the hydrolysis of enzymes in senescent leaves and relocation of nitrogen to new vegetative growth or reproduction.

However, suppose these deficiencies could be made good, and that it therefore becomes possible to estimate the marginal efficiency of nitrogen investment. The estimate would be empirical. Studies of the foliage and its function could not, in themselves, suggest 'why' it should take any particular value. It might seem that a way forward is to treat nitrogen and carbon economy as a symbiosis, balancing the amount of nitrogen invested in carbon acquisition against the amount of carbon invested in roots, and used in nitrogen acquisition, reduction, and protein synthesis. Then two problems would emerge. One of them is readily apparent: the analysis would draw in other aspects of economy in the plant, each having its own undetermined marginal efficiency. A single, example, that of water economy, will

suffice. The function of root systems in nutrient uptake cannot be divorced from that of water uptake (Hari et al. 1990, Hof et al. 1990). The economies of nitrogen and water are inter-related above ground too, through the action of stomata (Buckley et al. 2002).

The second problem, perhaps better termed a restriction, is fundamental to the application of optimality theory. There can be no independent criterion of marginal efficiency in any function within, or of, a living organism. An attempt is made to support this assertion via the following discussion of plant water-relations.

4 Efficiency of Transpiration

Stomatal movements have been investigated for two hundred years, but progress has been slow. No single response is fully understood at the cellular level. The stomatal complex remains a 'black box'. Attempts to define its characteristics empirically by means of multi-factorial experiment have not been fruitful. The complexity, including as it does, a diurnal rhythm and numerous interacting sensitivities to plant internal and external factors each with particular dynamic characteristics, is overwhelming.

Yet, in general terms, the 'purpose' of stomata and stomatal movements has always seemed clear: to effect a compromise between the 'needs' of a plant to assimilate carbon dioxide and to avoid desiccation. It is revealed by a variation in stomatal aperture frequently observed during clear days. Stomata open widely in the morning when light is sufficient to promote rapid photosynthesis, but humidity deficit, and therefore potential rate of transpiration, is relatively small. They tend to close during the middle of the day and early afternoon, when the humidity deficit is greatest, and sometimes open more widely for a short period in the late afternoon before closing as the light fades. The effect of all this is to increase the amount of carbon-dioxide taken up corresponding to the amount of water lost.

The relevant paradigm of optimality is formally similar to that for nitrogen. It is that the function $A_T - \kappa \cdot E_T$ be maximum, E_T being rate of transpiration, E , integrated over the same period of

time as rate of assimilation. (The period should be taken as sufficiently short not to encompass significant change in the amount of soil water available to the plant.) The new, undetermined multiplier, κ , the marginal efficiency of transpiration, is not entirely analogous to that relating to nitrogen use. Whereas nitrogen was regarded as a fixed investment, E is to be treated as a variable cost, dynamically controlled by stomatal movement. Therefore optimality requires that $A - \kappa \cdot E = A_T - \kappa \cdot E_T$, or

$$\partial A / \partial E = \kappa \quad (6)$$

at all instants of time and, also, over all elements of the foliage of a plant. (Early treatments of the problem used the expression $\partial E / \partial A = \lambda$, this being the marginal efficiency of carbon fixation in terms of water use. It matters little. There is no gold standard in plant economy.)

Under what conditions should the criterion be tested? Consider two extremes. A constant diurnal variation in stomatal aperture of the kind observed on a clear day would go some way towards fulfilling the optimal requirement. If that were the sole characteristic of stomatal movement, then the only feasible test would be to see whether the stomatal variation is appropriately matched to the climatic variation during a 'typical' day. It is plain however that the stomatal complex is capable of actively responding to the variables that make climate different from day to day. Is it any good at calculus of variations? In principle, fluctuations in E and A resulting from small, frequent endogenous fluctuations in stomatal aperture could be used to adjust the mean aperture so as to maintain $\partial E / \partial A$ virtually constant. If the stomatal complex had that capacity, then it would be legitimate to test it in conditions quite atypical of those occurring in the natural environment. The possibility must probably be rejected. Stomatal apertures do, at least in some circumstances, exhibit endogenous fluctuations, but the characteristic period seems much too long to fulfil an information-seeking role.

Yet some investigations have, in effect, presumed that stomata do explicitly sense and control $\partial E / \partial A$, for they have involved subjecting plants to conditions quite foreign to those occurring naturally. Often, one environmental factor is varied

while all others are held constant; and the temporal pattern of the variation imposed is usually artificial too. Absolute humidity is the variable frequently chosen. Certainly, stomata respond to changes in humidity, and the way they do so is of interest. Nevertheless absolute humidity does not vary much (unless precipitation occurs) during the course of a day. It is variation in humidity deficit that is important, and that is dominated by variation in temperature.

The optimisation hypothesis, relating as it does to the ideal adaptation of stomatal behaviour to a putative selection pressure, can only be tested in the circumstances in which we think adaptation has occurred. Perhaps there is something to be learnt from animal ethology. As Medawar (1965) put it, until the 1930's it was supposed that, 'even poking an animal would surely be better than just looking at it'. But then there came a 'new behavioural concept to ponder on: the idea that an animal might in some way apprehend a sensory pattern or a behavioural situation as a whole and not by a piecing together of its sensory or motor parts. That was the lesson of *Gestalt* theory.' Most of us would feel that a *Gestalt* concept of stomatal behaviour is a stop-gap, merely awaiting success of a mechanistic explanation. Yet if the primary interest is in the way which higher plants cope with the exigencies of the terrestrial environment then a holistic description of stomatal behaviour is a mechanism. A physiological effect is an ecological cause.

However, the hypothesis is difficult to test when the environment is allowed to vary, or caused to vary, in ways that occur naturally. It is necessary (as with all optimisation analyses) to estimate the repercussions of something being not as it actually is; in this instance the effect on E and A of a small increase or decrease in stomatal conductance, g say, to gas diffusion. If one were able somehow to artificially superimpose small periodic fluctuations on the natural variation of conductance (see Cardon et al. 1994, 1995) then one could in principle acquire the necessary information (vid. previous remarks about 'explicit' sensing of $\partial A/\partial E$). In practice, the effect of doing so is estimated by using knowledge, from ancillary experiments, of A as a function of irradiance, temperature, and leaf internal CO_2 pressure. An approximate treatment sets

$$A = k \cdot (c - \Gamma)/(1 + 1.6k/g) \text{ and } E = g \cdot \delta \quad (7)$$

k being an internal light and temperature-dependent 'conductance' to carbon dioxide fixation (primarily depending on the activity of ribulose-bisphosphate carboxylase when irradiance is large), c and Γ ambient and temperature-dependent compensation concentrations of carbon dioxide, and δ ambient humidity deficit. The factor 1.6 is the ratio of the diffusion coefficients of vapour and CO_2 in air. It is assumed that the effect of leaf boundary layer is so small that leaf temperature may be taken as air temperature. Differentiating these relations with respect to g (that is, determining the effect of a virtual fluctuation in g) and setting $(\partial A/\partial g)/(\partial E/\partial g) = \kappa$, it follows (Cowan 1977) that

$$\frac{A}{E} = \sqrt{\frac{(c - \Gamma) \cdot \kappa}{1.6 \cdot \delta}} \quad (8)$$

The corresponding expressions for A , E and g are readily found. They have been tested in near natural conditions with some success (Hari et al. 1999, Koskela et al. 1999). However a few qualifications need to be mentioned.

Stomatal movements are much too slow to react optimally to rapid changes in physical environment, such as the variation of irradiance associated with broken cloud. Some plant movements are relatively very fast. Why are stomatal movements not quicker? It has been calculated (Cowan 1982) that the benefit, in terms of carbon assimilation, of an optimal variation of stomatal aperture, as compared with constant stomatal aperture, is no more than a few percent. Perhaps the energy expended in frequent, rapid movement would exceed the additional benefit. Perhaps the potential additional benefit is too small to have influenced selection. However, to invoke such an 'explanation' brings one close to the dilemma defined by Lewontin.

With broad leaves and low windspeeds it is necessary to take account of the leaf boundary layer. In some circumstances the effect may have an importance far beyond complication of the formal analysis. When atmospheric temperature is very high, the increase in leaf temperature consequent on stomatal closure may cause irreversible, or

temporarily irreversible, damage to the photosynthetic system. Then there is a new constraint on optimal stomatal behaviour. In the words of Raschke (1975) the leaf faces the alternatives of thirst or heat-stroke.

The most important caveat relates to predictability of physical environment. Of course, it is precisely because physical environment is not fully predictable that plant carbon and water economy may derive benefit from the active responses of stomata. On the other hand, if the physical environment were thoroughly unpredictable, maintaining $\partial E/\partial A$ constant at a predetermined value would be of little benefit, for the future consequences of doing so in terms of accumulated gain of carbon and loss of water would be unpredictable also. The problem could be ameliorated if κ were to be continually adjusted in the light of past consequences, that is to say by some form of integral control. The way stomatal behaviour might be advantageously influenced by previous accumulation of plant carbon (or perhaps the pool size of a particular metabolite) is probably too difficult a question to address profitably. The complementary question, how might it advantageously respond to accumulated loss of water, is more tractable, and will be addressed next.

5 Efficiency of Soil Water Use

Any attempt to establish a paradigm of efficient use of soil water by a plant should incorporate at least the following four considerations. Two of them suggest a plant should assimilate and therefore use up water as quickly as possible as long as soil water is available. First, rainfall is unpredictable. If the reservoir of soil water is not fully used before it is replenished, opportunity has been lost. Second, there are other calls on soil water. If a plant does not use the soil water available to it rapidly a greater proportion of it will be used in other ways, including uptake by the roots of neighbouring plants.

On the other hand there are two exigencies suggesting a plant should be somewhat parsimonious in its use of water. First rate of assimilation does not increase linearly with rate of transpiration.

A given amount of water brings a greater return in terms of assimilate if used relatively slowly. Therefore an 'on:off' pattern of use is inefficient. Second, the slower the rate at which water is used, the less is the likelihood the plant will be afflicted by drought. The risk that drought will ensue becomes progressively greater as soil water content diminishes. Stomatal closure will not protect a plant from drought if the 'available' soil water is almost exhausted, because some water continues to be lost through the plant cuticle.

This last consideration is the most difficult to take into account, for it requires that the deleterious effects of drought be defined. To use some arbitrary, or empirically determined function for the effect of water 'stress' on growth metabolism does not seem justifiable. There is no clear reason why metabolism should be affected while turgidity is maintained. It is perhaps profitable to consider extreme cases. In one (Mäkelä 1996), drought is taken to cause no more than a temporary cessation of growth. The other is germane to discussion of fitness and survival. It is assumed that metabolism is not at all affected until soil water content declines to a critical level at which the plant dies. Optimal use of soil water is then provided by the variation of E_T with soil water content that maximises the function

$$\bar{A}_T - v \cdot K \quad (9)$$

in which \bar{A}_T is the probable average rate of assimilation over an extended period of time, K is the risk that drought will occur within the same period, and v is a new undetermined multiplier. There have been two attempts to formulate the relationship between \bar{E}_T and K in terms of the statistics of rainfall, and thence to find the form of the required variation (Cowan 1982, 1986). In the first, it is assumed that every rainfall is sufficient to saturate the root zone. The second avoids that assumption, but is mathematically flawed. It is hoped to publish a rigorous analysis soon. However the analyses are of restricted value, for they assume that the development of the plant is sufficiently slow for its architectural and physiological characteristics to be taken as constant. They would thus apply, if at all, only to a mature shrub or tree in which assimilate is primarily used to make good the losses due to respiration,

leaf senescence, herbivory, and reproductive processes. They do not take account of the most obvious consequence of assimilation: the progressive increase of plant size, both above and below ground. In neglecting this they conspicuously fail to deal with that period when a plant, following its emergence as a seedling, is perhaps most vulnerable to drought.

Suppose, for heuristic reasons, that these difficulties could be overcome: that optimal stomatal behaviour in, say, an annual plant can be described, as a function of climate, soil water content and ontogenetic development. Then, in place of an average rate of assimilation over an arbitrary period of time, it is possible to deal with the probable accumulated growth, G , of a plant at maturity. And K is appropriately defined as the probability that a seed will either not germinate or that the seedling will die before reaching maturity. (The fact that failure to germinate has nothing to do with stomatal behaviour will be of no concern, since the derivative $\partial K/\partial x$, where x represents any characteristic of stomatal behaviour, can be taken to exist.) The function to be maximised is now

$$G - v \cdot K \tag{10}$$

with v being yet another undetermined multiplier. Hence optimal control of water use is that for which $\partial G/\partial x = v \cdot \partial K/\partial x$ or, in brief,

$$\partial G/\partial K = v \tag{11}$$

in which the implicit parameter is x .

The question now is, what determines v , the marginal benefit of risk?

6 The Nexus

If the circumstances and behaviour of all the individuals of a species were identical, then any appreciable level of risk would extinguish the species before many generations had passed. A species that occupies a uniform niche exists precariously. The risk that the individuals of a species can 'afford' to sustain will depend on the extent to which the risk to the species is spread; for example by geographic dispersal of seed, and

temporal dispersal of its germination.

It cannot therefore be supposed that each individual will be ideally adapted to the environment to which it has been consigned. Nevertheless, let us proceed by supposing that the species as a whole is somehow represented by an individual that is perfectly adapted. If the number of seed produced at maturity is proportional, by the factor α , to the growth made, then the (Malthusian) ratio of the numbers of individuals in successive populations is

$$M = \alpha \cdot G \cdot (1 - K) \tag{12}$$

The relationship provides the means to obtain an empirical estimate of the multiplier v , for maximisation of M with respect to any characteristic x requires

$$\partial G/\partial K = G/(1 - K) = v \tag{13}$$

It is now worth noting that the implicit parameter x need not refer only to a stomatal characteristic. It could equally well be root:shoot ratio. Nor need it be confined to a characteristic to do with water economy. It could refer to any attribute affecting both G and K , for example the synthesis of secondary compounds (including proteins in some species – Shewry and Lucas 1977) that provide defence against pests and pathogens. The relationships between G and K will, in general, differ for different attributes, but if they are optimal each of them should conform to Eq. 13. It seems, then, that the equation is a terminus for numerous routes of optimal analysis. It hardly seems necessary to point out that there will be optimality considerations involving α too, particularly in its compromise, via seed size, with K .

But on reflection the equation appears devoid of meaning. For any identifiable species or subspecies that exists, or ever existed, M must at one time have exceeded unity. Later, if the population becomes quasi-stable, it can only hover about unity. Intra-specific competition (direct or indirect) will see to that. It follows that Eq. 13 is a truism. An adaptation that increases one of the three factors, α , G , or $(1 - K)$, must, while increasing the density or spread of the population to a new level, eventually cause a diminution in one or both of the other two. These factors,

either singly or in combination, do not constitute a measure of fitness, or a criterion of optimality. One might say of two species coexisting in the same geographic location, but having very different combinations of α , G , and K , that they are adapted to, that is to say fittest within, their respective 'niches'. However the term niche, used in that way, is simply a surrogate for a particular combination. Of course, Eq. 12 is suitable only for annual plants with determinate reproduction. But whatever more detailed devolution of M into factors may be appropriate to plants with more complex life histories, the general tenor of these observations will remain true.

7 Conclusion

What can one learn from the sequence of undetermined multipliers μ , κ , ν , and ν ? There were two examples of optimisation which, arguably, produce useful and testable results. They are both to do with consistency; whether μ , a marginal efficiency of nitrogen, is the same for different enzymes, and for one, or a group of enzymes in different leaves. And whether κ , a marginal efficiency of transpiration, is the same at different times and in different leaves. However, as soon as one asks whether a marginal efficiency is, itself, optimal one embarks on a fruitless quest. Each attempt at an answer must appeal to a higher level of plant organisation. The simplifications required to make the problem tractable become increasingly dubious. And indeterminacy survives to reappear in another form. The final multiplier, ν , involves growth and survival, and can potentially be evaluated simply because the species exists. We are no further in explaining its magnitude.

The reason for the impasse is simple. The criterion for optimal efficiency of any system, that is to say the purpose for which the system is fitted, is not to be found within the system itself. It must be imposed from outside. But, for biological systems, there is no 'outside', because the external physical and biotic environment is not independent of the functioning of the organisms that inhabit it.

This has been something of a cautionary tale. It by no means refutes the usefulness of optimisa-

tion theory in plant physiology. It does however point to a general problem in its application. It is (as in the writing of this article) not so much how to begin as where to end.

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