Challenges and Opportunities of the Optimality Approach in Plant Ecology

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A meeting was held in Hyytiälä, Finland 10–12 April 2000 to assess critically the current challenges and limitations of the optimality approach in plant ecophysiology and botany. This article summarises the general discussions and views of the participants on the use of optimisation models as tools in plant ecophysiological research. A general framework of the evolutionary optimisation problem is sketched with a review of applications, typically involved with balanced regulation between parallel processes. The usefulness and limitations of the approach are discussed in terms of published examples, with special reference to model testing. We conclude that, regardless of inevitable problems of model formulation, wider application of the optimality approach could provide a step forward in plant ecophysiology. A major role of evolutionary theory in this process is simply the formulation of testable hypotheses, the evaluation of which can lead to important advances in our ecophysiological understanding and predictive ability.

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1 Introduction

Adaptation and acclimation have intrigued scientists ever since Darwin (1872) proposed his postulates of natural selection. It has become common practise to use evolutionary arguments to account for the form and behaviour of living organisms, and the scientific community has widely accepted the underlying principles as a cornerstone in modern biology. Claims that the theory cannot be falsified and is therefore unscientific (Popper 1974, Lewontin 1977, Gould and Lewontin 1979) have been overturned by recent advances in theoretical evolutionary biology, and methods of quantifying hypotheses involving adaptation have clarified the requirements of testing predictions of the theory (Pigliucci and Kaplan 2000). Nevertheless, Darwin's ideas have remained somewhat detached from advances in botanical and ecophysiological research. This may reflect doubt in some quarters that evolutionary theory can be transformed into a precise tool – optimality modelling – that provides important new insights and reliable, quantitative predictions.

The method of optimisation under evolutionary constraints has been at the centre of debate ever since Fisher (1930) presented his fundamental theorem of natural selection. Modern approaches assume that 1) individuals vary in particular structures/functions, 2) at least part of such phenotypic variation is heritable, and 3) individuals vary in fitness (the rate at which they produce viable offspring per unit time) at least partly as a function of their heritable phenotypic differences (Lewontin 1970). Fitness depends on the environment in which an organism lives. Optimality models all assume that newly emerging structures/functions are constrained to some domain of variation, as a result of limits to phenotypic and genetic variation within a population or species, the amount of energy available to individuals, and fundamental physical and chemical laws.

From these premises, if heritable structures and/or functions arise that increase the fitness of their bearers relative to others, individuals bearing such structures/functions will increase in frequency and the population as a whole will evolve toward a greater average in relative fitness. This implies that individuals should evolve toward the highest peak in the adaptive landscape of fitness by phenotype, at least if the pattern of genetic inheritance is relatively simple and if drift, mutation, recombination, or migration is large enough to move populations off local peaks and onto the slopes of global maxima (Fisher 1930, Williams 1970, Hofbauer and Sigmund 1988, Frank and Slatkin 1992). This process has also been extended beyond biology in "evolutionary algorithms", which have been shown mathematically to maximize "fitness functions" by varying one or more control parameters through "mutation" and "recombination", and then allowing "selection" to allow a climb of the implied adaptive landscape (Goldberg 1989, Bar-yam 1997).

As a quantitative approach, optimality models can provide an important means for analysing the consequences of different plant forms and functions. Often, such models ask how variation in one or more traits would affect carbon gain and, hence, plant growth and presumed competitive ability in a particular environment (e.g., see Horn 1971). However, a number of criticisms have been raised regarding the premises and implementation of such models. One salient issue is the proper recognition of key physical and biological constraints on optimisation. Gould and Lewontin (1979) argued that the degrees of freedom left for selection to optimise are often minor compared with the historical, phylogenetic "*Bauplan*" (developmental architecture) that constrains the kinds of new forms which might emerge. But competition (and, hence, selection) can operate across lineages with different *Baupläne*, and phylogenetic constraints – which were simply asserted by Gould and Lewontin – can be operationally difficult to identify in many cases (Givnish 1986a, 1997). More generally, the nature of the available genetic variation within a population or species – including patterns of linkage, epistasis, and pleiotropy, and constraints imposed by the rates of mutation, recombination, and migration – may not allow a globally optimal trait to evolve. Although optimality can be mathematically shown to occur in simple, one locus-two allele systems, organisms actually inherit structures and functions in a more complicated fashion, which need not imply the optimisation of individual traits (Cheverud 1988). A suggested solution to this latter problem has been to include constraints related to the correlation between the trait considered, and other properties (Cheverud 1988, Baatz and Wagner 1997).

The problems of constraints are related generally to our incomplete ability to define a comprehensive model of the functioning of the organism in its natural environment. However, this is not different from the construction of any model. Models are always simplifications, but as such, they often help us understand the essential. If the theory of evolution is regarded fundamental for biology, utilising its ideas in model building should likely improve our understanding of some of the essential characteristics of living organisms.

A meeting was held in Hyytiälä, Finland 10–12 April 2000 to assess critically the current challenges and opportunities of the optimality approach in plant ecophysiology and botany. While this special issue of Silva Fennica contains a selection of the papers presented, this article aims at summarising the general discussions and views of the participants on the use of optimisation models as tools in plant ecophysiological research. We take the view that, regardless of inevitable problems of model formulation, wider application of the optimality approach could provide a step forward in plant ecophysiology, both for giving new insights, and for developing predictive models of plant structure and function. To argue for this, we review the optimisation method on the basis of some published models, with special attention to the types of problem treated, the applicability, and the limitations of the method.

2 Optimisation Models: a General Framework

The optimisation approach was introduced into plant ecophysiology in the 1970s by a number of authors (Mooney and Dunn 1970, Williams 1970, Horn 1971, Givnish and Vermeij 1976, Cowan 1977, Orians and Solbrig 1977, Givnish 1978, 1979, Honda and Fisher 1978). Since then, a variety of problems have been analysed in an evolutionary optimisation framework (e.g., the collection of papers in Givnish 1986b). Some models follow the abundance of phenotypes through generations, assuming rules for the reproduction and survival of different forms (Hofbauer and Sigmund 1988), but these are beyond the scope of this paper, in which we take a functional/optimal rather than a population approach.

The optimisation method can be formulated in terms of (1) a plant trait x, varying in a domain X, (2) environmental (driving) variables u, (3) a model of plant function f, dependent on x and u, and (4) a fitness function F, dependent on f. The problem is expressed as finding $x \in X$ that maximises F under the constraints on plant function in the environment u. If the success of plants with a particular trait depends on the frequencies of other morphs in a population, the optimisation problem should be formulated as an evolutionary game (Givnish 1982, Maynard Smith 1982), but this will not change the essence of the arguments.

It is crucial that the specification of all components of the preceding model be consistent with our understanding of the process of natural selection and plant functioning. The trait x must be heritable, but (at least for single-trait models) it is not necessary to understand precisely how the trait is inherited. Environmental effects u on the function f are either predictable (in which case they can be included in the optimisation as a dependence of f on u), or unpredictable (in which case they are untouchable, by analysis or natural selection). Plant functions f which affect fitness F and are under plant control (e.g., stomatal conductance, root-shoot ratio) are most often expressed in terms of energy or dry matter – both of which, conveniently, map directly to fixed C in plants, and both of which should directly affect plant growth, survival, and competitive ability. Of course, this is never the whole story – external and phenological factors are important as well – but those can be characterized empirically and treated as constraints on the optimisation.

Typical applications of the optimisation method include problems of resource allocation, e.g. optimal timing of seed production (Mirmirami and Oster 1978, Vincent and Pulliam 1980), allocation between height and diameter growth (King 1981, Mäkelä and Sievänen 1992), and

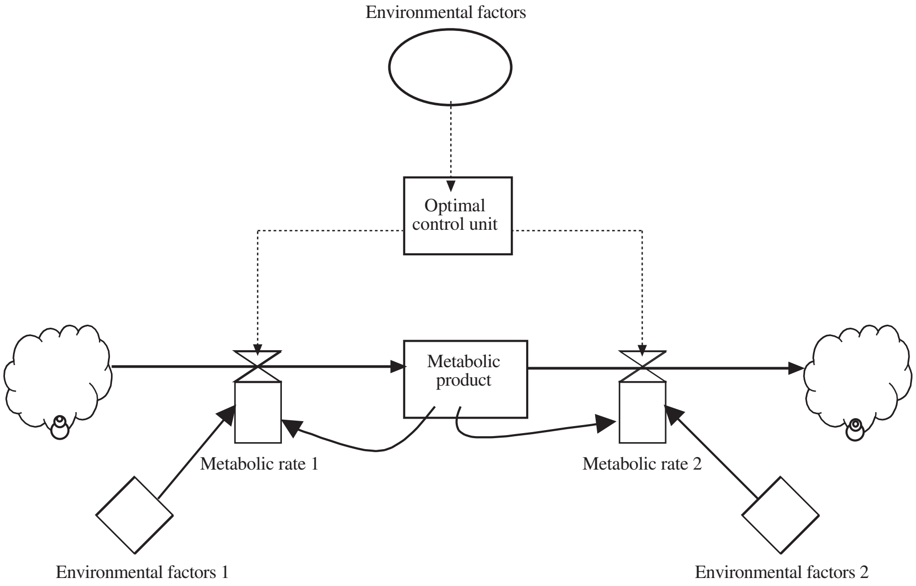

Fig. 1. Schematic presentation of the use of optimisation in plant growth models. In addition to material flows regulated by state variables and environmental driving variables, a control unit is assumed that feeds information to the metabolic system.

allocation between shoot and root (Givnish and Vermeij 1976, Givnish 1979, Reynolds and Thornley 1982, Tilman 1988). Some examples involve achieving a functional balance between parallel processes, e.g., as a result of balancing nutrient uptake and carbon assimilation without a waste of construction material (Reynolds and Thornley 1982), the optimal allocation of nitrogen in the canopy (Field 1983, de Pury and Farquhar 1997), or the optimal balance between photosynthesis and transpiration (Cowan 1977, Cowan and Farquhar 1977, Hari et al. 1986). Although more frequently used in animal studies, evolution under competition between members of a species has been studied using game theory (Vincent 1977, Rose 1978, Givnish 1982, Mäkelä 1985). Game-theoretic approaches are required when the presence of competitors, or of specific competitors, qualitatively changes the identity of the best strategy. For example, in herbs, the leaf height that maximizes growth in the absence of competitors (i.e., zero, corresponding to basal leaves) is the one that minimizes growth in their presence, and the game-theoretic optimum increases with the density of competing coverage (Givnish 1982).

Directly or indirectly, all applications of the optimality principle are somehow involved with establishing a balanced regulation of parallel metabolic processes. Such processes and related plant structures have thus been regarded as constraints to the problem. The underlying assumption seems to be that metabolic processes, such as photosynthesis, nutrient uptake or transpiration, are governed by some fundamental physical or chemical laws that do not allow for much variation. Similarly, qualitatively new structures will not arise easily. For example, Cowan (1977) argued that a membrane that is permeable to CO_2 but not to water vapour, would be highly adaptive, but it has never evolved. Any passive structure that can permit the passage of large, heavy, slow-moving CO_2 molecules will almost inevitably allow smaller, lighter, faster-moving H_2O molecules to pass as well (Givnish 1979). On the other hand, the modellers hypothesize that the biochemical or hormonal regulation balancing the different processes within the existing types of structure shows enough variability to allow for evolutionary adaptation. Similar assumptions have been used in studies of animal adaptations, where the optimality of wing or body shape has been analysed (Maynard Smith 1982).

It is important to recognise that solutions of the optimisation problem do not yield any information about the actual developmental mechanisms responsible for generating an adaptive trait or pattern of acclimation to particular conditions. Instead, they produce a functional relationship between the driving variables, state of the plant, and the control variable, that yields a prediction of optimal behaviour. From this perspective, biochemical or hormonal regulation can be regarded as a black-box superimposed on the metabolic system, functioning so as to make the different metabolic processes interact optimally with respect to fitness (Fig. 1). Most of the published optimality considerations involving metabolic models can be viewed in this general framework.

In theory, the fitness function F should be defined as the potential rate of reproduction by an individual. But variation in fitness can be difficult to observe, especially in long-lived organisms such as trees, and the impacts of variation in different traits on fitness can be difficult to disentangle. Thus, a general fitness function cannot easily be defined, let alone tested. In practice, models usually stipulate that fitness F is directly related to a quantity $\hat{F}$ that is intuitively thought to influence reproductive success, assuming that the specified function is monotonically correlated with the fitness of an individual (Parker and Maynard Smith 1990). The most common substitutes for fitness are derived from the energy or carbon balance, including whole-plant carbon gain (Givnish and Vermeij 1976, Givnish 1979), photosynthesis (Cowan 1977) or growth rate either momentarily (Reynolds and Thornley 1982) or over a period (Mäkelä and Sievänen 1992), actual or a proxy of seed production (Vincent 1977, Mäkelä 1985), and combinations of various goals simultaneously (Cowan 1977, Cowan and Farquhar 1977, Givnish 1986c, Hari et al. 1986, Mäkelä et al. 1996). Some studies use more indirect indicators of the potential carbon gain, such as the height growth rate of an individual (King 1981).

3 On the Applicability of Optimisation Models

3.1. Feasibility of Premises

Models are generally applicable if they can provide realistic descriptions of the phenomenon in question. The applicability can be analysed 1) by assessing the suitability of model premises for each particular problem, or 2) by testing model predictions against the real system. For the applicability of optimisation models, we discuss two aspects of the premises of the theory that may reduce the applicability of the method for certain problems.

Firstly, the optimisation method assumes that the characteristic in question affects the fitness of an individual. If this is not the case, we cannot assume any optimality about the feature. For example, it seems clear that the colour of pine bark is irrelevant for the fitness of pine trees, and can therefore not be explained as a solution to an optimality problem. While in many cases, the assessment of significance relative to fitness appears fairly straightforward, sometimes our inability to judge the importance may be a serious limitation to the applicability of the method.

Secondly, the optimality method assumes that once a characteristic bears significance for reproductive success, the process of variation and selection – under phylogenetic constraints, if necessary – will eventually lead to an adapted structure. Whether or not such a structure will be achieved largely depends on the rate of mutation. If an equilibrium cannot be achieved while the selective pressures due to the environment remain stable, there are no grounds for assuming optimality of a particular phenotype.

Kickowski (1998) showed that the mutation rate leading to chlorophyll deficiency in mangroves is about 0.004 per haploid genome per generation. Since there are about 300 genes that can cause the deficiency, the frequency becomes about 10^{-5} per gene per generation. Kickowski also showed that marginal populations have higher mutation rates than those in central populations. He graphed data of Koski and Malmivaara (1974) showing similar trends in Pinus sylvestris and Picea abies growing in Finnish forests.

Because self-pollination occurs in *Rhizophora mangle*, the red mangrove populations are in near mutation/selection equilibrium in ca. 5 generations. Most tree species are outcrossing and the mutation rate of 10^{-5} would mean that the time required to go half way to equilibrium is 110 generations, assuming that the mutation is completely recessive lethal and mating is at random. The number of years required to establish an appropriate mutation/selection equilibrium may in many cases exceed the length of time that the population's present habitat has existed, e.g. many boreal and temperate habitats that were under ice less than 10 000 years ago.

The discussion above is on a per gene basis and refers to lethality. Presumably mutations that are adaptive take much longer, as the selection will not be as rapid. The frequency of adaptive mutations is also likely to be much less than that of lethal mutations. Drake et al. (1998) suggest that mutation rates in higher eukaryotes are currently indistinguishable from 1/300 per cell division per effective genome (which excludes the fraction of the genome in which most mutations are neutral). Given that there are at least 20 000 genes per effective genome in plants, the rate becomes 1/6 000 000 per gene, per cell division. This would appear to be at least 60 times slower than the estimate of Kickowski above, given that not all mutations relating to chlorophyll synthesis will be lethal. The discrepancy is reduced when one considers that there can be several cell divisions per generation. Nevertheless, the large number of base pairs per gene (ca. 10^3) means that the mutation rate per base must be of the order of 1 in 10^8 to 10^9 per base per generation.

The fact that evolution and adaptation has occurred presumably reflects the large numbers of individuals in successful populations. For example, with say 10^3 individual trees per hectare, a million hectares is sufficient to experiment with a particular base in one individual in an average generation time.

3.2. Model Testing and Evaluation

For a model to be applicable either as a scientific tool increasing our understanding, or as a means for prediction, we should be able to assess how closely it portrays reality. It has sometimes been assumed that evolutionary optimisation models intend to be logical derivations from the theory of evolution, and that their validity should ensue from that of the theory. However, because the optimum phenotype in any given model depends on the particular assumptions it makes relating performance to a certain set of control variables, and relating fitness to performance, each model can yield different predictions. Differences among these models are not tests of the underlying hypothesis of adaptation (see Maynard Smith 1982, Givnish 1986a), but of the validity of the assumptions made regarding the functional relationships among plant traits, performance relative to a particular criterion, and fitness. Therefore, although each is inspired by the same, general evolutionary principles, individual optimisation models should be each regarded as independent hypotheses to be evaluated through empirical testing.

The method of model testing largely depends on the purpose of the model. If model building has simply been motivated by scientific curiosity – e.g., to find out what would be an optimal structure or function, given the current understanding of the processes – the result is likely to be a qualitative model, and a satisfactory test can just be to observe the same qualitative traits in the real world. In this sense, optimality models provide a means of moving from our current understanding of the functional determinants of, say, photosynthetic rate and whole-plant growth, to why plants have stomata, why species in moist, fertile environments have broad leaves and heavy allocation aboveground, and why species with different sets of biological equipment are distributed in different environments.

Some interesting applications of qualitative optimality models deal with the ecological strategies of plants adapted to different environments. These plants can be different ecotypes of the same species, or different species. Horn (1971) helped pioneer this approach, comparing single-layered and multilayered tree crowns, asking how different crown forms would perform along a gradient from sun to shade, and showing that the optimal number of leaf layers increases with irradiance. Hänninen (1996) compared different provenances of Scots pine in a common garden model using optimality principles. Also, a number of studies have been trying to understand optimal water use strategies of trees but have yielded varying success (Palmroth et al. 1999, Li et al. 2000). Kikuzawa (1991) used a simple optimality approach to predict leaf longevity on a global scale (but see Givnish 2001 in this symposium). Examples of a game-based approach include the continuous, analytical models of Givnish (1982) and Mäkelä (1985) for optimal plant height in herbs and trees, respectively. Tilman (1988) extended this kind of approach by simulating competition among model old-field plants assumed to differ in their energetic allocations to leaves, roots, and stems, and in their leaf nitrogen concentration and photosynthetic rate.

The optimality method can also be used to produce more quantitative, predictive models of plant processes. This often involves developing a deep and rapid understanding of the regulation of processes involving several interacting biochemical processes and responses to environmental conditions. Traditional approaches to this kind of problem would require a long, painstaking analysis of myriad biochemical processes, together with a huge – and quite likely impractical – series of experiments exploring responses to a factorial set of environmental conditions. An alternative might be to analyze how allocations to different pathways should be adjusted to maximize energy gain as a function of environmental conditions, which would lead directly to predictions of how overall performance of a process should vary with those conditions. No guarantee can be made that optimisation will provide an accurate answer, but it does provide an attractive alternative approach for developing a series of working hypotheses.

That this approach can indeed yield applicable models with simple, yet biologically sound structures, has perhaps been best illustrated by the development of the optimal gas exchange hypothesis (Cowan 1977, Cowan and Farquhar 1977, Givnish 1986c, Hari et al. 1986, Mäkelä et al. 1996). The model maximizes the daily carbon gain of the plant under minimum transpiration (given a certain "cost" of water in units carbon) by predicting optimal time course of stomatal control, regulated by those environmental variables that affect photosynthesis and transpiration. The resulting model structure is simple, yet rather general and biologically sound. Furthermore, it has been shown to produce surprisingly accurate predictions of the daily course of photosynthesis, transpiration and stomatal conductance in extensive field tests (Berninger et al. 1996, Hari et al. 1999, Hari et al. 2000).

An often-overlooked limitation to the applicability of optimisation models arises because they are inevitably based on the observed operation of underlying physiological mechanisms – which themselves are presumably adapted to the conditions under which the plants which bear them evolved. This means that if the external signal detection and internal signal transduction apparatus which governs acclimatory behavior have evolved under a specific set of conditions, they may cue development of non-optimal phenotypes if an organism is placed in an alien environment. This certainly seems to be the case for CO_2. Another example, the optimal stomatal control model (Hari et al. 1986) predicts that during typical summer days, the stomata are regulated by light intensity and water vapour deficit. Both of these driving variables have a typical diurnal pattern. Even if the model performs well under these typical conditions (e.g. Hari et al. 1999), it is possible that the actual mechanism of stomatal control is not based on these factors, but on something else that would normally produce the same, optimal response. There is no automatic guarantee that the response remains optimal if the conditions become atypical, such as in the laboratory, or during active spells in wintertime when the contribution of photosynthesis to the annual carbon balance is minute. From this perspective, optimisation models resemble empirical models; they can be regarded as predictive tools under the conditions in which they have been tested.

However, even if there is no guarantee that behavior will remain instantaneously optimal if the environment changes, the optimisation paradigm implies that the mean behavior will move towards the optimum, if it is at all subject to natural selection. This is where optimisation moves forward from ordinary models: it identifies the direction in which a property will change, rather than, necessarily, the present value of that property. It can be used to infer the causal origin of present states, or to predict the direction in which those states will change if the causal forces change.

4 Concluding Remarks

When any theory is used as a basis for building a model, reality is simplified from the outset, partly to facilitate logical deductions and mathematical calculations, and partly to allow a focus on the implications of one or more key traits. Deductive reasoning based on a few, simple postulates is a dominant feature of many models in physics and chemistry, but the inherently far greater complexity of biological systems requires a greater emphasis on simplification. It has been argued that, given the difficulties in formulating and testing postulates, evolutionary theory should simply not be used in ecophysiological research (e.g. Thornley 1991). However, the argument that evolutionary models are insufficiently detailed would, in principle, apply to any model, and indeed, to almost any form of scientific analysis or prediction. As Dobzhansky (1973) noted, “nothing in biology makes sense except in the light of evolution”, so it seems particularly ill-advised to banish evolutionary thinking from ecophysiological research.

The optimisation models reviewed above have successfully avoided falling into the trap of the “adaptationist programme” cautioned by Gould and Lewontin (1979) and successors. The models have not aimed at proving that a trait is an adaptation, but considered, given the domain of possible solutions and their functional significance, what the trait *should* be like *if* it was optimal. This method leads to testable hypotheses about the optimality of the trait in question under the constraints hypothesized, and the model provides a quantitative tool for assessing the role of constraints *vs* selection in relation to particular traits. If the model can be shown to represent reality fairly, it can be used to make predictions, just like any other model that can be tested against data. The method can also be used for analysing what would happen, at least in the short term, if selective pressures were modified as a result of environmental change.

As we have pointed out above, the added value of the optimisation method is perhaps greatest in deriving predictive models for cases where the balancing of parallel processes has not been understood mechanistically, or involves underlying processes that are too complicated to be understood from any practical point of view. In such cases, the optimisation method can actually be regarded as a method of simplification, parallel with other methods such as linearisation or statistical analysis. Optimisation is based on the unifying principle of ecology and biology – natural selection and evolution – and is therefore the most appropriate clarifying and simplifying tool available.

The motivation for the special issue at hand, as well as the Hyytiälä workshop as a whole, was to assess the current challenges and opportunities of the optimality approach in plant ecophysiology and botany, through a wider exchange of information and opinion. We have demonstrated that the method can be fruitful for both giving insights into how living things work, and for predictions of their responses to the environment. However, because use of the theory always involves a deep understanding of the processes underlying plant function, competition, selective pressures, and the evolutionary constraints – for all of which there is no general schema as yet – the method is by no means a simple machine that automatically produces useful or realistic models of plant function on a production-line basis. Each model must be carefully considered and tested, incorporating the best insights available in physiology, ecology, and evolutionary biology. A major role of evolutionary theory in this process is simply the formulation of testable hypotheses, the evaluation of which can lead to important advances in our ecophysiological understanding and predictive ability.

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