ABOUT THE PERPETUAL STATE CHANGES IN PLANTS APPROACHING HARMONY WITH THEIR ENVIRONMENT[1,2]

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ABSTRACT

The adaptation of plants to a continuously changing environment is approached as an expression of an optimisation strategy, dictated by the thermodynamic demand for minimal entropy production. A logic bridge between the theoretical predictions of open system thermodynamics and the phenomenology of experimentally investigated aspects of the behaviour of plants is established, in terms of the J-K-B-Trilogy, and further applied for the photosystem II of the photosynthetic apparatus. The chlorophyll a fluorescence kinetics, analysed according to the Theory of Energy Fluxes in Biomembranes, lead to a constellation of structural and functional parameters, thus providing a quantification of the system behaviour. A case study in Camellia leaves is then treated on the basis of these theoretical considerations. Different light-adapted states were induced in these leaves and the multiparametric response of the system to short-term changes of the light intensity was studied. It is demonstrated that this response is indeed in accordance with the theoretical predictions.

Key-words: Thermodynamics of irreversible processes, Open systems, Adaptation, State changes, Optimality, Harmony, Stress, Photosystem II, Chlorophyll a fluorescence kinetics.

INTRODUCTION

The present work is a conceptual approach of the adaptation of plants to a perpetually changing environment. The theoretical considerations are further linked with a case study in Camellia leaves, where fluorescence kinetics serve as the tool for an insight into the photosynthetic machinery.

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Our arguments concerning adaptation appeal to the "why", not to the "how"; they deal with reasons, not with mechanisms. The latter, though a limitation, permits them to go beyond the studied organism and be related with wider and more general theories and reasonings. Such a powerful theory is thermodynamics of irreversible processes (nonequilibrium thermodynamics), the reasonings of which have been further developed in the last decades for open systems and, moreover, extended in an attempt to be applied for the description of living systems (PRIGOGINE, 1947, 1967, 1980; KATCHALSKY & CURRAN, 1965; NICOLIS, 1990).

Though the field of thermodynamics of open systems is highly developed as such, it is, unfortunately, very seldom used or integrated in experimental biology. The goal of this paper is to illustrate that experimentally investigated aspects of the behaviour of plants are, often, in full accordance with the theoretical predictions for the behaviour of open model systems. Therefore, we accept here the challenge to select well defined expressions used in chemistry, physicochemistry and physics, which allow us to create a logic bridge between the theoretical predictions and the phenomenology of experimental signals.

Our arguments are based on the *JKB Trilogy Concept* (STRASSER, 1984, 1985, 1986a, 1986b, 1988; STRASSER & HAGNER, 1984), an approach that has been built up on such thermodynamic directives. This concept, without losing from its generality, has been formulated in a way that provides links with the bioenergetics of the photosynthetic machinery, both on the phenomenological and the biophysical level. These links are utilising the methodology based on the *Theory of Energy Fluxes in Biomembranes* (STRASSER, 1978, 1981; STRASSER & GREPPIN, 1981; SIRONVAL *et al.*, 1981).

Adaptation of plants to the perpetually varying environmental conditions is approached as an expression of the general adaptive and evolutionary behaviour of organisms. The adaptive strategies, considered as conditioned by thermodynamic constraints, are regarded to be successful when they provide for competitively effective pathways of thermodynamic flow. In this approach, the thermodynamic demand for minimal entropy production (PRIGOGINE, 1947) is considered to be dictating adaptation under a given constellation of environmental conditions (STRASSER, 1984, 1985, 1986a, 1986b, 1988).

THE THEORETICAL CONSIDERATIONS

WHY THERMODYNAMICS

The living systems are open thermodynamic systems in which irreversible processes occur. Although these systems exist frequently in time-independent states, they are not in equilibrium, since the flow of energy and matter does not cease. Hence, they cannot be described by classical thermodynamics. Moreover, they appear to defy the second law of thermodynamics, since they tend to produce order than disorder, i.e. to

decrease than to increase their entropy. This was a challenge for those who wished to apply thermodynamic reasoning to the living systems.

The development of linear nonequilibrium thermodynamics has provided a formalism which appeared suitable for their description, since this approach, being not based on any specific kinetic models for the processes considered, has great generality and is capable, in principle, of describing and correlating a wide variety of processes within a single theoretical frame.

Entropy Production by Irreversible Processes

Let us start with a simple system within which an irreversible process occurs and which exchanges only heat with its surroundings. According to classical thermodynamics, the second law is stated as: $TDS \geq \Delta_e Q$, where $\Delta_e Q$ is the net heat exchanged between the system and its surroundings, ΔS the resulting change in the entropy of the system and T the temperature at which these take place. The equality applies when the process is reversible and the inequality when the process is irreversible. If the system under consideration was isolated, i.e. if $\Delta_e Q = 0$, the law would be expressed as $T\Delta S \geq 0$. Anyhow, this case is not of interest for living systems because in them the energy exchange and even the matter exchange never ceases.

The current theory of thermodynamics of irreversible processes restates the second law by splitting the change in the entropy of the system, ΔS, in two terms: $\Delta_e S$, the change due to entropy exchanged between the system and its surroundings and, $\Delta_i S$, the change due to entropy created by irreversible processes occuring within the system:

$$\Delta S = \Delta_e S + \Delta_i S$$

The first term is directly associated with the net heat exchange $\Delta_e Q$, as $\Delta_e S = \Delta_e Q/T$. It can thus be positive or negative since $\Delta_e Q$ can be an input or an output respectively. On the contrary, the second term expressing entropy production is by definition never negative; it is positive for irreversible processes and vanishes in the case of reversible processes which, anyhow, are not likely to occur in nature.

Concerning the surroundings of the system, their entropy change, ΔS_{sur}, is only due to the heat exchange which, for them, is equal to $-\Delta_e Q$. So,

$$\Delta S_{sur} = -\Delta_e Q/T = -\Delta_e S.$$

Consequently, the entropy change of the universe (i.e. of system + surroundings), ΔS_{univ}, is equal to $\Delta_i S$ and, therefore, always positive for irreversible processes:

$$\Delta S_{univ} = \Delta S + \Delta S_{sur} = (\Delta_e S + \Delta_i S) + (-\Delta_e S) = \Delta_i S$$

Already with this restatement it is clearly shown that the total entropy change ΔS of a system can be negative (provided that the system is not isolated, so that $\Delta_e S \neq 0$), but the entropy change of the universe, ΔS_{univ}, is always positive. This means that when a

system, as it happens with living systems, increases its order and complexity, this does not defy the second law because, nevertheless, the entropy of the universe increases.

Dissipation of Free Energy

The arguments we have above summarised deal only with the entropy changes. However, these changes correspond to energy changes which have to obey as well the law of conservation of energy. Let us use again a simple model within which a single irreversible process occurs and take, as an example, that this process is an exothermic reaction

$$R \rightarrow P \; + \; |\Delta H|$$
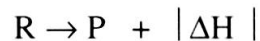
where R are the reactants, P the products and ΔH the change in enthalpy resulting from the difference between the enthalpy content of the reactants and the products:

$$\Delta H = H_P - H_R$$

The released energy, $|\Delta H|$, can be further transformed to work + heat. However, the enthalpy consists of two components:

$$H = TS + G$$

The first, associated with entropy, is under isothermal conditions an *unavailable energy* in the sense that it can not be transformed to work, while the second is defined as an *available energy* and is, therefore, called *free energy (Gibbs energy)*. Thus,

$$\Delta H \; = \; H_P - H_R \; = \; T(S_P - S_R) \; + \; G_P - G_R \; = \; T\Delta S^{irr} \; + \Delta G \; = T\Delta_i S \; + \Delta G$$

or, since ΔH is negative,

$$\Delta G \; = - \; |\Delta H| - T\Delta_i S$$

This shows that the free energy decreases and, even more, that only a part of this decrease can be indeed used for work while another part is spent for entropy production. This *dissipation of free energy* is referred usually as *devaluation or degradation* of energy, based on a consideration that useful energy is only the energy available for work.

Open Systems and the Dissipative Function

So far we have used a simple system which produces entropy at the expense of its own free energy, since the only energy that it exchanges with its surroundings is heat. Open systems, however, exchange matter as well. They "import" reactants, transform them by irreversible processes to products which they then "export". By these processes they produce entropy reducing the free energy of their surroundings.

In the case of open systems we use the term *rate of entropy production*, d_iS/dt, since we refer to a continuous flow of matter and energy and a consequent continuous

entropy production. Thereafter, the quantity Td_iS/dt expresses the rate of dissipation of free energy and it is called *dissipation function* Φ. This function has been related quantitatively to the irreversible processes occuring within the system as:

$$\Phi = Td_iS/dt = \Sigma J_k X_k \geq 0$$

where J_k is the *flux* (rate) of the k-th irreversible process and X_k is the *conjugate force* causing that flux.

So, the demand of the second law for increase of entropy is expressed as a requirement that the sum of the products (*fluxes* • *forces*) is greater than zero, not necessarily that each individual term is positive. Thus, some of these terms may be negative, provided that the positive terms are sufficiently large so that $\Phi \geq 0$. A negative term expresses decrease in entropy associated with production of order or complexity, and a positive term, associated with devaluation, expresses decrease of order or complexity. Thus, devaluation provided by metabolic processes can make possible an entropy reducing process leading to the development of organisation i.e. to structuring and complexification of a system, via appropriate coupling between the processes.

Considerations of *dissipative structures* are indeed applicable to living systems. Biological systems build up their complex structure and maintain a high degree of internal order by dissipating entropy to their surrounding at the expense of free energy. In other words they convert free energy into organisation.

When an open system is at a time-independent state, it means that all its state parameters are constant and so is its entropy, i.e. its conformation, structure and concentration of constituents. This can be written as:

$$dS/dt = d_eS/dt + d_iS/dt = 0$$

However this does not mean thermodynamic equilibrium because entropy production continues to occur. The entropy of the system remains constant by adjusting $d_eS/dt = - d_iS/dt$, i.e. by exporting entropy to the surroundings with the same rate that it produces entropy. These time-independent states in open systems are called *steady-states or stationary states*.

One of the most important insights of nonequilibrium thermodynamics is that for dissipative structures (open systems) the *stationary state* is that state in which the entropy production, d_iS/dt, assumes the minimal value consistant with the restraints imposed (PRIGOGINE, 1947). This is equivalent with minimal dissipation of free energy. Thus, these states are the *optimal* ones and the system tends to achieve and maintain them. In this sense they are states of *stability* and they are, therefore, considered to play a role in the thermodynamics of irreversible processes similar to that played by the states of equilibrium in classical thermodynamics.

A summary of the presented basic considerations of thermodynamics of open systems is shown in Fig. 1.

ADAPTATION AS A THERMODYNAMIC NECESSITY

If the stability thresholds of a kinetic pathway for dissipation is exceeded, the system converts to new *kinetic modes* which must, in turn, achieve a new steady-state, i.e. a new state for minimal dissipation of free energy. The trend towards decreasing this dissipation reflects the tendency for the transition between kinetic regimes to lead in the direction of increasing efficiency in the utilisation of energy for biomass production. So this principle does not prescribe activity but rather describes what occurs in consequence of that activity (WICKEN, 1987).

In living systems *state changes* leading to *adaptation* can, therefore, be regarded as dictated by a thermodynamic necessity (STRASSER, 1985). Ordinary physicochemical systems have a precise stoichiometric kinetic pathway for energy conversion and, thus, their performance is strictly modulated by the imposed conditions. In living systems mechanisms regulating the internal thermodynamic forces that govern physiological processes have been erected to prevent such, deterministic, responses to external conditions.

We are witnessing here an expression of the dialectics between structure and function. *Biological organisation has no meaning apart from the function it serves: The structure controls the function and the function informs the structure.*

MORE ABOUT OPTIMA

The exhibition of an optimum in the response of a system towards varying external factors is a widely spread, even a common, phenomenon: from the well-known in every-day life optimum speed for maximum efficiency in the performance of a car engine, up to examples from enzymology, like maximisation of enzyme activity at a certain pH or at a certain temperature. It is worth of to make here some clarifications concerning the terms *optimum* and *maximum:*

First, depending on the choice of the dependent variable, optimisation can be revealed by exhibiting a minimum and not a maximum, e.g. minimal dissipation is equivalent with maximal conservation. Therefore it would be preferable to use the general term *extremum.*

Second, *optimum* is associated with the independent variable (in the examples mentioned, the car speed, pH, temperature) and it refers to the value of this variable for which the dependent variable (efficiency, activity) reaches an *extremum. Optimum,* however, has not necessarily to refer to a quantity, but it can also characterise a situation corresponding to a maximality or minimality of a system parameter, i.e. to a condition quantitatively defined. For example, a thermodynamically *optimal* state is that for which entropy production is *minimal.*

The third clarification is not simply dealing with terminology but it is a conceptual distinction that applies for physiological functions and evolutionary success. For an ordinary conservative physicochemical system, optimum performance is achieved by

maximisation of efficiency, which means complete extraction of the *free* energy, the *Gibbs energy*. However, according to classical thermodynamics, this implies complete reversibility which can only be succeeded when the process advances with infinitely slow net rates. Obviously, this maximum associated with such a constraint - representing equilibrium of a stable system - cannot be optimum for life. On the contrary, this optimum requires a proportioned balance between efficiency and irreversibility, i.e. a limited reduction of efficiency. Thus, efficiency is a system parameter to be optimised and not at all maximised.

According to GNAIGER (1987) efficiency can be regarded as the *fitness function*, which is optimised in order to maximise fitness, expressed by an appropriate *fitness parameter*. Every modification of a fitness function towards the optimum is an *adaptation*, since fitness refers to the response to the environmental conditions. In other words, adaptation is the optimisation of a fitness function to maximise a fitness parameter under a defined set of constraints. Which the fitness parameter and what the specific optimum value is, depends on the physicochemical relationships which dictate the need for the best compromise between efficiency and irreversibility.

The aim of this clarification is to point out, using efficiency as an example, that, generally, a system parameter can play either the role of the parameter to be maximised or that to be optimised, depending on the needs of the system and the conditions. Moreover, the constellation of needs and conditions determines what is the *best compromise* and to the maximisation of which system parameter this does reflect. For example, four such parameters - output functions *(net flow, output power, economic flow, economic output power)* have been derived by STUCKI (1982) in his analysis of oxidative phosphorylation.

THE J-K-B TRILOGY

Any living system is an open system, with a complex structure, that functions as energy convertor. The actual performance of the system at a given time has been described by Strasser (STRASSER, 1984, 1985; STRASSER & HAGNER, 1984) as determined by three terms:

J - all energetic inputs,

K - the constellation of structural - conformational parameters that determine the kinetic pathways for energy conservation and dissipation. This constellation corresponds to the biochemical inventory and the conformation, i.e. to the hardware of the system and it is, therefore, an extensive parameter.

B - the established relative level of the energy flow through the system. So B is an intensive parameter and can be regarded as an expression of the behaviour of the system.

This approach, proposed by Strasser, is the basis of the J-K-B Trilogy Concept (STRASSER, 1985, 1986a, 1986b, 1988). It can be formulated as

$$\eta = f (J, K, B)$$

where η is an expression of the actual performance of the system.

Since B is controlled by K and J, the three factors can be reduced to two, provided that the function $B = f (K, J)$ is known. What this function could be, depends on the model by which the system is described. Moreover, if K remains constant, then $B = f(J)$, and the performance of the system can be considered as a function of B only, i.e. $\eta = f(B)$. This function is the *state function* of the system for the given K; each K defines another state function. Thus, the conversion of the system to a different *kinetic mode* can be equivalently ascribed as a shift to a different *state function,* or as a *K-change.*

ADAPTATION IN TERMS OF THE J-K-B TRILOGY

Let us now see how the thermodynamic demand for minimal entropy production - minimal dissipation is expressed through the J-K-B trilogy. We have mentioned above, in thermodynamic terms, that a living system is not restricted to function through a unique kinetic mode for energy dissipation and that, if the thresholds of stability, under certain imposed conditions, are exceeded, it then turns to new kinetic modes which permit the achievement of a new stability.

Since the kinetic mode is determined by structure, turning to a new kinetic path means that a change in structure has occurred which, in the frame of the J-K-B trilogy, is translated as a change in K.

We have analysed above that for a living system the *optimal* state is the *stationary* or *steady state*, i.e. the state where dissipation is minimal. Compared to what? To all other possible states corresponding to the same K and different J and B, i.e. expressed by the same state function. This optimal state is, therefore, realised by a unique pair of J and B for a certain K. However, B is not an independent variable; it depends on both K and J. Let us now suppose that we start watching the system when it is at such a state. If J changes then B changes. If the extent of the changes is so small that it does not deviate the system from the optimum, there is no need for the system to make any adjustment, i.e. the thresholds of stability have not been exceeded. But if the change in J and the consequent of B are such that the system deviates from its optimum, the new position cannot be considered thermodynamically as a state to be maintained. The system has been led to *suboptimality* (STRASSER, 1988) and it has to overcome it. It can neither change the external factor, i.e. the environmental conditions J, nor the resulting behaviour B; it has, however the capability to change its structure, i.e. the K term. This is an advantage of living systems over ordinary conservative systems which are obliged to perform with a given, fixed state function, i.e. with a constant K, and, thus, their activity is strictly stoichiometrically defined by the input J.

The above analysis can be visualised by the multiparameter presentation of $\eta = f (J, K, B)$, as shown in Fig. 2. The combination of $\eta = f (J)$ and $B = f (J)$ leads to the derivation of the *state function* $\eta = f (B)$. In this figure two sets of $\eta = f (J, K, B)$

curves are presented, corresponding to two different states denoted by the K_1 and K_2 values. K_1 refers to the state adapted at J_1, and K_2 to the state adapted at J_2. This is demonstrated by the fact that the curve $\eta = f(J)$ for $K = K_1$ has its maximum at $J = J_1$ and, similarly, the curve $\eta = f(J)$ for $K = K_2$ has its maximum at $J = J_2$. Equivalently, J_1 is the optimal J for $K = K_1$ and, J_2 the optimal J for $K = K_2$. These optimal values define accordingly two optimal values for B: B_1opt and B_2opt.

The optimal constellations of η - J - B are marked in Fig. 2 with open symbols. Deviation from the optimal constellations, induced by J changes, leads to suboptimal constellations (marked with closed symbols). The constellations corresponding to J_1 or J_2 are presented respectively by circles or squares. The heavy line with the arrows shows the response of the system to a cyclic environmental change $J_1 \rightarrow J_2 \rightarrow J_1$. It is clearly shown that the way from J_2 to J_1 is not the reversed of that from J_1 to J_2 This means that a reversible environmental change provokes a cyclic state change walk.

For the living systems two modes of changes can thus be distinguished:

* Moving within one state function corresponds to changes of the system actual performance, resulting from the immediate B - changes, i.e. the changes in the behaviour, driven by changes in the input J. Such movements, being the immediate response to stress, lead to *suboptimality.*

* Moving from one state function to another, corresponds to conformational changes, i.e. to K - changes, driven by suboptimality. These movements, expressing adaptation, lead to *optimality.*

The K-change is, however, not abrupt, and the search for the new K is a "walk" via changes of K, consequent changes of B and resulting changes of energy dissipation, until a constellation of JKB is achieved which corresponds to a new stability, a new optimum. This constellation is the *attraction point* for the *state change walk,* leading to a state adapted to the new environmental conditions. The cyclic change in Fig. 2 (heavy line with arrows) represents two such successive walks: state 1 $\rightarrow$ state 2 and state 2 $\rightarrow$ state 1.

OPTIMALITY AS HARMONY

We have analysed above that for each state function there is a value of B for which the system is at its thermodynamically optimal condition. The system is then in *harmony* with its environment. This term, introduced by STRASSER (1988), reveals the dialectics of optimality pointing out that optimality refers to the relation - interaction of the system with its environment. Any change in the environmental input causes a disturbance of the achieved harmony and leads to *disharmony* with the environment. For the system this situation reflects *suboptimality.* Because of the thermodynamic demand for optimality, this suboptimality creates a *state change force* under which the system undergoes state changes, i.e. changes in its conformation, until a new constellation of conformational parameters, a new K, is reached which brings the system to a new opti-

mality. Then the state change force vanishes and a new stability, a new *harmony* with the environment is established.

THE STRESS CONCEPT

Though the term "stress" has been exactly defined in mechanics, concerning biology it has been given widely differing meanings. Probably due to an extension of the physical meaning, many of them converge in attributing "stress" to any environmental factor "unfavourable" for the living organism under consideration (LEVITT, 1980). In accordance, the ability of the organism to survive the unfavourable factor has been called "stress resistance".

Our approach, referring to plant physiology, is however different in principle. As proposed and analysed by STRASSER (1988) the concept of *Stress and Stress Adaptation* can be integrated in the same conceptual frame as our above stated arguments, based on reasonings of nonequilibrium thermodynamics and dissipative structures. It is thus regarded as a dynamic relation between organism and environment, keeping from the physical approach the concept of *action-reaction*, and offers the possibility of analytical description and quantification.

We consider that *stress* has a relative meaning, with the *non-stress* as the reference condition. More precisely, we consider *stress* as a deviation from the *non-stress* situation. The latter is not statically but dynamically defined: it is the situation at which the plant is in harmony with its environment or, equivalently, the plant is at its thermodynamically optimal state - the state of minimal entropy production. In other words, *non-stress* corresponds to optimality and stress to suboptimality. Accordingly, a *stressor* is every factor which provokes a stress, i.e. which leads to suboptimality. *Stress adaptation* is the sequence of processes which realise the state changes that lead to a new optimality, a new non-stress situation, a new harmony with the new environmental conditions. Any physical or chemical change occuring during these state changes has been denoted as *strain*.

However, the environmental conditions never cease to manifest alterations and, thus, the system is *perpetually* undergoing *stress - stress adaptation* processes, searching and approaching harmony with its environment.

In this concept, no environmental factor is considered *a priori* as unfavourable and the plant has not to "resist", but it simply reacts. As far as the system manages to adapt, which means that the attraction point is within realistic limits (STRASSER, 1988), stress is not only harmless but, even more, *constructive* because it results in improved resistance and adaptive evolution. But, if the adaptability of the system is overtaxed, then stress is *destructive,* leading to permanent damages or even to death, as stated by LARCHER (1985, 1987). This duality has been called *eu-stress* and *distress* by LICHTENTHALER (1988).

THE OPTIMUM WALK

The two curves $\eta = f(J)$ in Fig. 2 refer to two different states, state 1 and state 2, which are the states that the system attains when J is equal to J_1 and J_2 respectively. We can generalise this description considering that, instead of J we can have any environmental factor - E_1 and E_2 respectively - and , instead of η, any expression - let it be Y - of the system activity. We can further denote as $^1Y = f(E)$ and $^2Y = f(E)$ the curves corresponding to K_1 and K_2. So, when $E = E_1$ the adapted system is at the optimum 1, which means that ^1Y assumes its maximum value, denoted by $^1Y_1$. Similarly, when $E = E_2$ the adapted system is at the optimum 2 and ^2Y assumes its maximum value, $^2Y_2$. The *stressor* $\Delta E = E_2 - E_1$ drives the system to suboptimality leading it to the position $^1Y_2$. So, the system is now under stress; the amplitude $\Delta Y_{stress} = {}^1Y_1 - {}^1Y_2$ can be regarded as a measure of the stress intensity. The attraction point is the optimum 2 and, therefore, the difference $\Delta Y_{state} = {}^2Y_2 - {}^1Y_2$ is a measure of the state-change force that drives the system to its new optimum.

In Fig. 3 four curves are presented: $^1Y = f(E)$, $^2Y = f(E)$, $^3Y = f(E)$, $^4Y = f(E)$, corresponding to the adapted states to E_1, E_2, E_3 and E_4. Their optima can be accordingly denoted as $^1Y_1$, $^2Y_2$, $^3Y_3$ and $^4Y_4$. Let us now consider a change of the environmental factor form E_1 to E_4. In the figure we show two different modes for this change. The one is an abrupt change and the *stressor* is $\Delta E = E_4 - E_1$. The system is led to a suboptimality widely apart from the optimum $^1Y_1$ and the measure of the stress intensity is $^1Y_1 - {}^1Y_4$. The other mode is by stepwise changes, $E_1 \rightarrow E_2$, $E_2 \rightarrow E_3$ and $E_3 \rightarrow E_4$, with enough time after each of them to permit adaptation before the next one occurs. In other words, the *stressor* is applied as a sequence of doses, $E_2 - E_1$, $E_3 - E_2$ and $E_4 - E_3$, and the corresponding stress intensities are, $^1Y_1 - {}^1Y_2$, $^2Y_2 - {}^2Y_3$ and $^3Y_3 - {}^3Y_4$. The *state change walk* is now consisting of suboptimisations and optimisations occuring alternately and the extent of the deviations to suboptimality is obviously smaller.

If the doses of the *stressor* become infinitesimally small, i.e. if the change of the environmental factor is proceeding slowly, as it happens with the natural changes in a regular day, then the state changes tend to follow the *optimum walk*. By this we do not just imply that it is a walk on the line of optima but, much more, that it is, itself, indeed optimum, since the system can adjust without suffering from large deviations into suboptimality. This means that the effort of the system to be reorganised at the expense of free energy is the minimal.

The state change walk from $^1Y_1$ to $^4Y_4$ is different than that from $^4Y_4$ to $^1Y_1$ in all cases except when they both follow the path of the *optimum walk*. However, the process following the optimum walk cannot be considered as a true thermodynamically reversible one, where the expense of energy would be zero. According to the term *quasi-static process* which refers to a succession of equilibrium states, this process, being a succession of stationary states, can be characterised as a *"quasi-stationary process"*.

THE J-K-B TRILOGY FOR THE PHOTOSYNTHETIC MACHINERY

Let us now focus on the photosynthetic machinery and, more precisely, on photosystem II. We are dealing with an *energy convertor,* which is an *open* system, a *dissipative structure,* as shown in Fig. 4: absorption - flux of photons, trapping - flux of excitons, electron transport - flux of electrons, biological activity - flux of molecules. Besides this path of energy conservation, we also show the path of energy dissipation on the exciton level, i.e. heat dissipation and fluorescence, as well as the path of energy migration, such as spill-over, i.e. energy migration from PSII to PSI, and connectivity or grouping, i.e. energy migration between antennae of different photosynthetic units of the same photosystem.

Conservation, dissipation and migration are controlled via the corresponding rate constants, k_P (for photochemistry), k_D (for heat dissipation), k_F (for dissipation through fluorescence) and k_X (for any migration), which are determined by the structure and architecture of the system. This constellation of structural - conformational parameters are integrated in the K - term of the J-K-B trilogy. J, standing for all energetic inputs, corresponds to the excitation rate which, according to the *Theory of Energy Fluxes in Biomembranes* (STRASSER, 1978, 1981; STRASSER & GREPPIN, 1981; SIRONVAL *et al.,* 1981), is the sum of the directly absorbed photon flux and all possible fluxes of exciton transfer to the system. B, the dynamic behaviour, being a measure of the overall flow level, is expressed by the redox state of the reaction centers (RC), i.e. by the fraction of closed - reduced RCs.

Based on the *Theory of Energy Fluxes in Biomembranes,* formulae for the energy fluxes - both per reaction center RC and per cross section of the sample CS - and for the flux ratios or yields have been derived using experimental values (see Strasser & Strasser, 1995). The set of these parameters is also shown in Fig. 4. The constellation of their values at any instant can be considered as expressing the function of the system.

CHLOROPHYLL *a* FLUORESCENCE KINETICS: AN INSIGHT INTO STRUCTURE AND FUNCTION

Photosystem II, the open system under consideration, is however in a plant. We need a signal to get an insight into a complex component of an even more complex system. Fluorescence, though representing a very small fraction of the dissipated energy flux, has been proven to be a very useful, non invasive tool for this insight. A lot of information has been driven throughout the last six decades from such transients (for reviews see, PAPAGEORGIOU, 1975; BRIANTAIS *et al.,* 1986; KRAUSE AND WEIS, 1991).

A more recent way of detecting the signal (STRASSER & GOVINDJEE, 1991,1992; STRASSER *et al.,* 1995) has provided an even more thorough glance, since the measurements scan the time range of the fast phase with a time resolution of $10\mu s$ for the first 2 μs and of $1\mu s$ thereafter. This permits a much more precise detection of F_0, the fluorescence value at the onset of illumination when all RCs are open (B = 0). Moreover, when the fluorescence kinetics from O to P (P: the point of maximum fluorescence correspon-

ding to maximum B) are plotted on a logarithmic time scale (Fig. 5), two more steps, denoted as J and I (STRASSER & GOVINDJEE, 1991,1992; STRASSER et al., 1995) are clearly revealed. The very initial slope, which offers a link to the maximum rate of photochemical reaction - when all RCs are open - can also be more precisely estimated.

All the functional parameters of Fig. 4 can be linked by phenomenological expressions with information provided by a transient like the one depicted in Fig. 5 (STRASSER & STRASSER, 1995).

Based on the *Theory of Energy Fluxes in Biomembranes*, expressions relating the conformational parameters k_N (= $k_D + k_F + k_X - k_{con}$, where k_{con} is the rate constant for connectivity) and k_P with phenomenology were also derived (HAVAUX et al., 1991a). More precisely, these expressions relate the nonphotochemical, k_N, and photochemical, k_P, rate constants with the measurements at the extrema of the fluorescence transient, i.e. at O and M, where M is the highest possible level of P, achieved with a saturating light intensity and, thus, corresponding to the maximum possible fraction of closed RCs, i.e. B=1. φ_{p0}, the maximum photochemical quantum yield (max. photon use efficiency), is also related with the same experimental signals and linked with these conformational parameters. The deduced expressions are shown in Fig. 6.

In the same figure it is shown, as well, the expression for q_N, the so-called index for *non-photochemical quenching*. Besides arguments (HAVAUX et al., 1991a) concerning the nomenclature for this parameter based on the fact that q_N is as much related to k_N as it is to k_P (*see* Fig. 6), we can, however, regard it as a *state change index*, describing quantitatively the Kautsky slow phase and assuming values in the range 0 to 1, where zero corresponds to starting conditions, e.g. dark adaptation.

THE CASE STUDY

The fluorescence transient that dark adapted leaves exhibit upon illumination consists of a fast polyphasic rise within 1s and a subsequent decline towards leveling which reflects the achievement of a steady-state (Kautsky effect, KAUTSKY & HIRSCH, 1931). Perturbations of this state can be caused by changes in the quality (STRASSER, 1985) or the intensity of illumination (SRIVASTAVA et al., 1995), upon which the samples exhibit a fluorescence transient which levels off at a new steady-state. This wavy transient can be interpreted as reflecting the sequence of events leading to adaptation, the *state change walk.*.

Steady-states established by adaptation to different light intensities are thus physiological states defined by a constellation of external parameters and internal responses. In our case study (TSIMILLI-MICHAEL et al., 1995) we induced such states in Camellia leaves by exposing them to different light intensities and we then investigated their behaviour using as a tool the polyphasic Chl *a* fluorescence rise (OJIP). For each adapted state the multiparameter pattern of functional and structural expressions has been monitored by varying for a short time the light intensity, to investigate whether they are

controlled by internal regulations and if and how optimisation processes are realised and revealed.

MATERIAL AND METHOD

Chl a fluorescence transients of intact leaves of several years old Camellia plants were measured at room temperature by a Plant Efficiency Analyser (PEA, built by Hansatech Ltd., King's Lynn, Norfolk, UK) and recorded up to 1s with a data acquisition rate of 10 μs for the first 2 ms (and of 1 ms thereafter) and 12 bit resolution (STRASSER et al., 1995). The fluorescence signal detected at 50μs after the onset of illumination was considered as the F_0. The transients were induced by different light intensities, denoted as *excitation light intensities* (I_{exc}) and expressed as % of the maximum light intensity provided by the light source (I_{max} = 600 W.m^{-2}). The leaves were at different adapted states induced by exposure for 2h to different light intensities, denoted as *adaptation light intensities* (I_{adp}), followed by a 30s dark interval before the measurement to ensure, as it was tested, the reopening of the reaction centers. The different adapted states are denoted by the corresponding I_{adp}, which is also expressed as % of I_{max}, the light source for adaptation being that of the measuring apparatus. All the measurements with the different I_{exc} for the same adapted state were done on the same sample with a 2min exposure to the certain I_{adp} in-between them. This exposure serves as readaptation, as it ensures the elimination of any disturbance of the adapted state that could be caused by the previous measurement, i.e. by the 1s illumination. The protocol of the experiment for each adaptation can be summarised as:

2h I_{adp} + [* 30s dark -1s I_{exc} - 30s dark - 2min I_{adp} - repeat with a new I_{exc} from*...]

RESULTS AND DISCUSSION

In Fig.7 we show, as an example, a set of the recorded OJIP polyphasic fluorescence transients on a logarithmic (and on a linear in the insert) time scale. The presented set consists of the transients induced by saturating intensity (I_{exc}=96%).

The pattern of the fluorescence yield values at the phases F_0 (50μs), F_J (2ms), F_I(30ms) and F_P (max), as a function of I_{exc} and for different light adapted steady-states, is presented in Fig. 8. This pattern is extracted from all measured combinations of I_{exc} and I_{adp}. When I_{exc} coincides with I_{adp}, the signals can well be considered as criteria for steady-state conditions. These signals are presented by open symbols in the full pattern of Fig. 8. Their dependence on I_{adp}=I_{exc}, more clearly shown in the insert of this figure, reveals a maximisation of all F_J, F_I and F_P , when the common value of I_{adp} and I_{exc} is 12%. The appearance of a maximum concerning the P-level is in agreement with earlier reports (SRIVASTAVA et al., 1995) where modulated techniques were used. Moreover, we observe here that this behaviour is not restricted to the P-level but exhibited by all the intermediate steps of the induction curve. However, we consider this maximisation as the result of the simultaneous increase of the fraction of closed centers

- due to the increase of I_{exc} and the decrease in the fluorescence yield per closed center
- due to the increase of I_{adp}.

To get some information about the structural changes occurring during adaptation, the photochemical k_P, and nonphotochemical k_N, deexcitation rate constants (in arbitrary units) were calculated according to the equations in Fig. 6 and are shown in Fig. 9. The index q_N, (the so-called non-photochemical quenching) is shown as well for comparison.

Focusing on the P level of the transients, which corresponds to the dynamic equilibration of the redox state , i.e. it reflects the *stationary non-equilibrium state,* we show in Fig. 10 in a 3-dimensional presentation (parameter versus I_{exc} and versus I_{adp}), the dynamics of the following functional parameters, as functions of I_{adp} and I_{exc}: In Fig. 10b the $1-V_P$, where V_P is the relative variable fluorescence; in Fig. 10c the energetic flux ratio or yield $\varphi_{pP} = TR_P /ABS$, where TR_P is the trapping flux and ABS the absorption flux; in Fig. 10d the trapping flux per cross section TR_P /CS. The fluorescence behaviour F_P, already shown in Fig. 8, is also included in this presentation (Fig. 10a), being the empirical parameter based on which the functional ones are derived.

The link of these parameters with the experimental values is shown in Fig. 11. Concerning the expression TR_P / CS it is calculated by the given equation in arbitrary values. However, the equation would hold for absolute values if I_{exc} could be replaced by J_{exc} (as in Fig. 12), where J_{exc} is the flux actually absorbed and utilised for excitation per cross section.

The whole pattern of these expressions, presented in Fig. 10; can be followed in terms of the JKB trilogy (Fig. 12). Illumination by I_{exc} of a duration as short as 1s cannot alter the established conformation K, here expressed by φ_{p0}, but only monitors the dynamic behaviour B, here represented by $1-V_P$: The stronger the I_{exc}, the smaller the $1-V_P$ and, consequently, the φ_{pP}. However, between the non-physiological limits of I_{exc} = 0 (zero input, maximum $1-V_P$) and I_{exc} = 96% (maximum input and $1-V_P = 0$), TR_P /CS is expected to show a maximum.

What is important is that this maximum appears at $I_{exc} = I_{adp}$, demonstrating that maximisation is indeed revealed, as predicted, when the conditions ensure adaptation, i.e. when the system is in non-stressed conditions. φ_{pP}, standing for the efficiency, is not maximised; it can well be interpreted as corresponding to the function to be optimised. Its optimisation is here conjugated with the maximisation of TR_P / CS . However, by monitoring φ_{pP} with the same I_{exc} at different states, it is demonstrated that it reaches a maximum when $I_{exc} = I_{adp}$. The maximisation is revealed already at this level because φ_{pP}, depending both on the φ_{p0} of the state and the monitored $1-V_P$, reflects directly the maximisation regulations.

The vertical cut at $I_{exc} = I_{adp}$ of the presented surfaces in 3-dimensions (heavy line), reveals the transition function from darkness to high light adaptation under steady-state conditions. It can thus be considered as the *optimum walk.* This walk, as it appears in the dynamics of TR_P / CS curve, reveals that, among the different I_{adp} and the consequent constellations of internal parameters, there is an optimum one, "the optimum of

the optima" at $I_{adp} = 24\%$. Whether this value is regulated by the growth conditions and to what extent it is determined genetically, needs further investigation.

Looking on the heavy lines revealing the *optimum walk* in the behaviour of all presented expressions in Fig. 10, independently if they are maximised or simply optimised, we can see that they are similar in one respect: the extent of the changes in the values of all expressions is much smaller moving on these lines than on any other line in the 3-dimensional graphs that reveals movements within a fixed state function.

CONCLUDING REMARKS

The case study in Camellia leaves demonstrates experimentally that adaptation can well be approached as an expression of *optimisation* procedures, revealed by the maximisation of a certain parameter expressing the system performance. This is in full accordance with the theoretical predictions of open system thermodynamics. Moreover, the characteristics of the optimum walk appear to be in very good agreement with the proposition that the deeper sense of a state change may be seen in the capacity of *thermodynamic buffering* against sudden changes in the environmental conditions (STRASSER & HAGNER, 1984). A strong buffering is observed as *homeostasis* (HAVAUX, *et al.*, 1991b) This means that biological systems which are capable to perform state changes, have an ability to adapt to new environmental conditions, without disturbing heavily the biochemical flows of the whole metabolism. Under such an approach, *stress* and *stress resistance* can be considered as corresponding to the perturbation of the system and its buffer capacity respectively. The mathematical description and, thus, the quantification of stress and biological state changes can further be developed.

RÉSUMÉ

Les plantes changent perpétuellement leur état pour se trouver en harmonie avec l'environnement. — L'adaptation des plantes à un environnement en perpétuel changement a été considérée comme étant l'expression d'une stratégie d'optimisation déterminée par l'impératif thermodynamique d'une production minimale d'entropie. Un lien logique a été établi dans le cadre de la trilogie J-K-B entre les prédictions théoriques, dérivées de la thermodynamique des systèmes ouverts, et la phénoménologie de différents aspects du comportement des plantes examinés de manière expérimentale. Par la suite, ce lien a été utilisé pour le photosystème II de l'appareil photosynthétique. Les

cinétiques de la fluorescence de la chlorophylle *a*, analysées en fonction de la Théorie des Flux d'Energie, ont livré toute une série de paramètres structurels et fonctionnels permettant de quantifier le comportement du système. Ces considérations théoriques ont été appliquées à un cas concret avec des feuilles de Camellia. Différents états d'adaptation à la lumière ont été induites dans ces feuilles et la réponse multiparamétrique du système face à des changements de l'intensité lumineuse de courtes durées a été étudiée. Il est démontré que cette réponse concorde effectivement avec les prédictions théoriques.

Mots-clés: Thermodynamique des processus irréversibles, Systèmes ouverts, Adaptation, Changement d'état, Optimalité, Harmonie, Photosystème II, Cinétiques de la fluorescence de la chlorophylle *a*.

FIG. 1.

Above   A flow diagram illustrating the energy transformations and entropy changes as well as the resulting flows, associated with an irreversible process occuring within an open system, as explained in the text. A chemical reaction from **A** as substrate to **B** as products is considered (index A and B).

*Below*   The equations for these changes and flows:

Equation 1   shows the distribution of energy differences according to the 2nd law of thermodynamics (Δ**H** for enthalpy, Δ**G** for free energy, and **T**Δ**S** for the entropic component, where Δ**S** the change of entropy and **T** the temperature in K). As an example, the values for ATP hydrolysis are indicated.

Equation 2   shows the rate of entropy change, **dS/dt**, of a system open to its surroundings as a resultant of different components. Index **i** refers to the production of entropy within the system and index **e** to the exchanges between the system and its surroundings. Index **Q** stands for entropy changes associated with heat dissipation. Index **P** specifies the entropy change defined by the difference between products and reactants (B and A) concerning the entropic component of their molecular energy content.

Equation 3   shows that the energetic efficiency of the system η is optimal when the dissipation function Φ is minimal. **W** stands for the work, supplied by the system, that is usable in any form.

$$H_A = G_A + TS_A$$
$$H_B = G_B + TS_B$$

Eq. 1
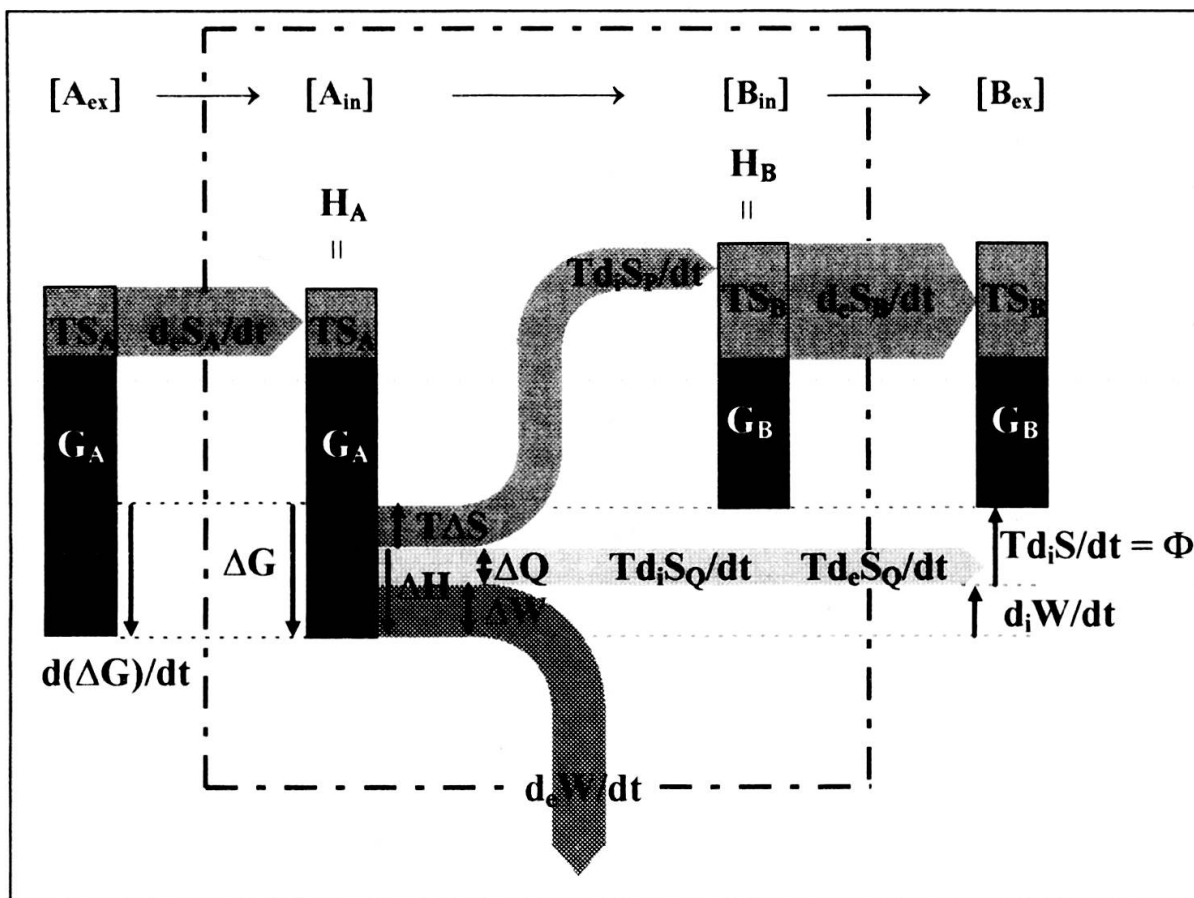
$$\Delta H = \Delta G + T\Delta S \qquad \textbf{2nd law}$$

$$(-15,5 \qquad -37,6 \qquad +22,2 \qquad for \quad ATP + H_2O \rightarrow ADP + P_i\,)$$

$$d_iS/dt = d_iS_P/dt + d_iS_Q/dt$$
$$d_eS/dt = d_eS_A/dt - d_iS_Q/dt - d_eS_B/dt$$

for steady state: $d_eS_B/dt = d_eS_A/dt + d_iS_P/dt$

Eq. 2

$$dS/dt = d_iS/dt + d_eS/dt = 0 \qquad \textbf{for steady state}$$

$$-d_eW/dt = -d(\Delta G)/dt - Td_iS/dt = d(G_A-G_B)/dt - \Phi$$

rate of work
done by the system

rate of free energy
transformed by the system

Eq. 3

$$\eta = 1 - \frac{\Phi}{d(G_A - G_B)/dt} \qquad \eta_{opt} \quad when \quad \Phi_{min}$$
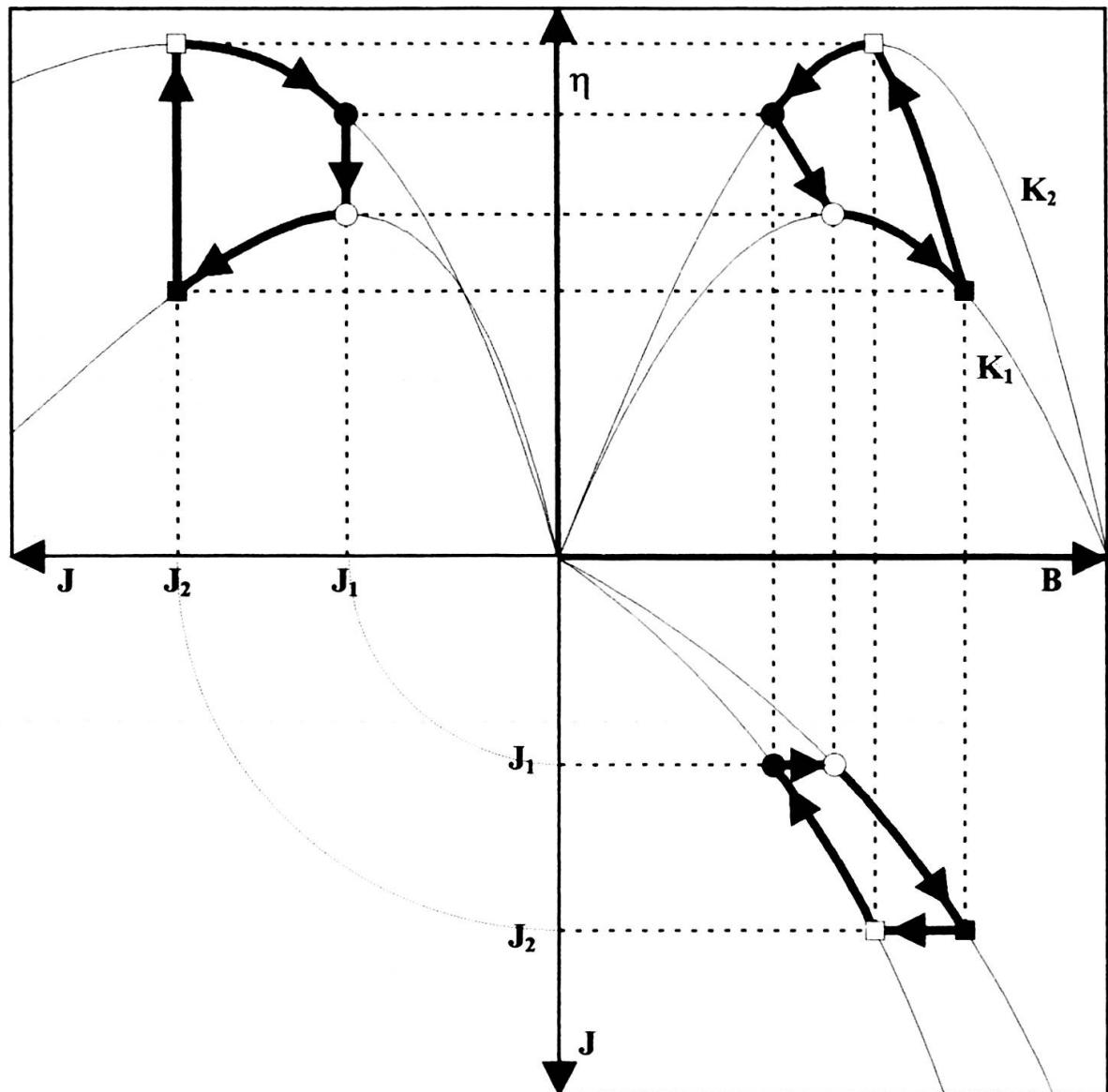
FIG. 2.

The multi-parametric presentation of η - B - J for two different states. J is the energetic input of the system, B its dynamic behaviour and η is a parameter expressing the actual performance of the system. The values K_1 and K_2 of the conformational term K denote the states adapted to the energetic inputs J_1 and J_2 respectively. The constellations corresponding to J_1 and J_2 are indicated by circles and squares respectively. Open symbols correspond to optimality and closed symbols to suboptimality. The heavy line with the arrows reveals the cyclic state change walk provoked by a reversible environmental change $J_1 \rightarrow J_2 \rightarrow J_1$.
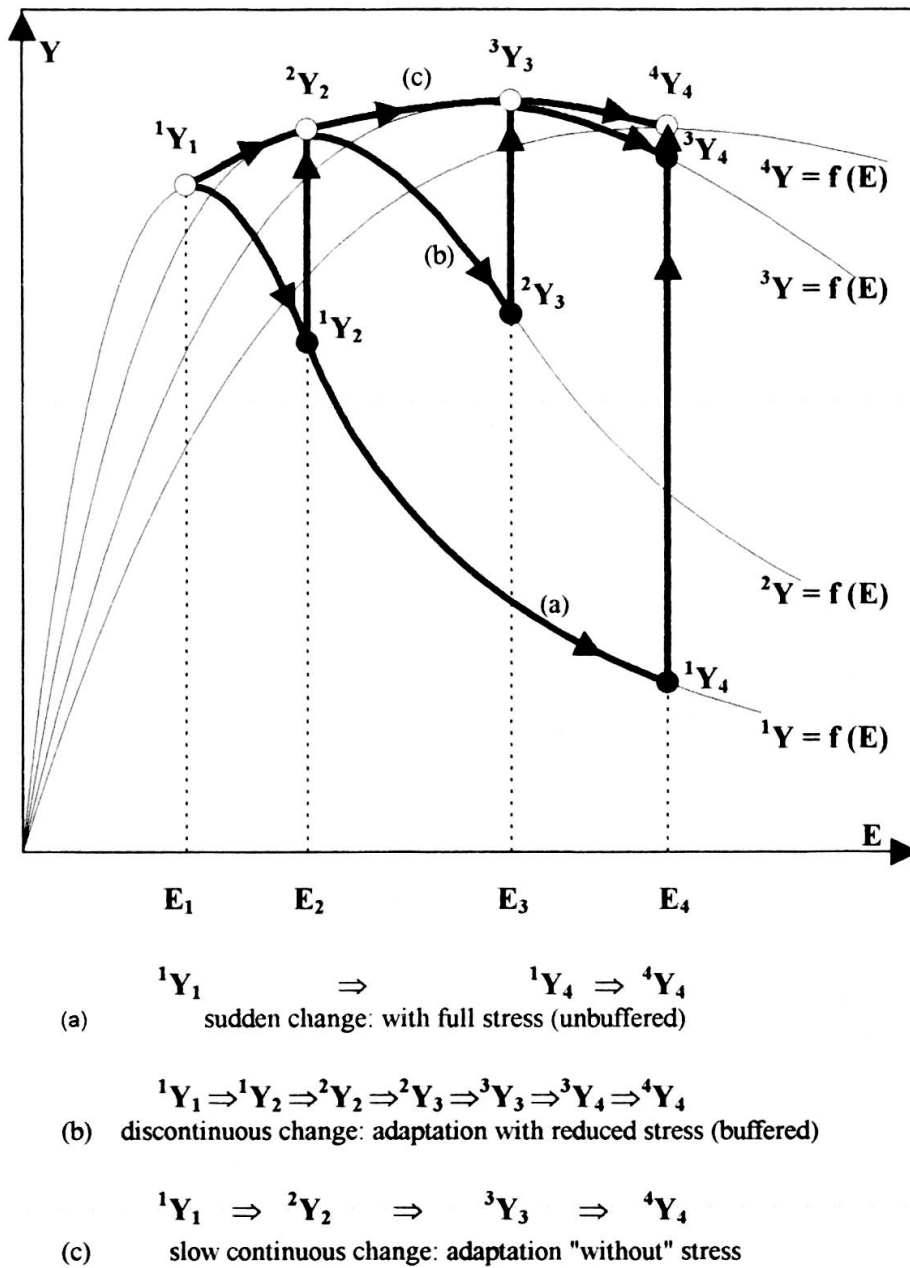
$$^1Y_1 \qquad \Rightarrow \qquad ^1Y_4 \Rightarrow ^4Y_4$$

(a)   sudden change: with full stress (unbuffered)

$$^1Y_1 \Rightarrow ^1Y_2 \Rightarrow ^2Y_2 \Rightarrow ^2Y_3 \Rightarrow ^3Y_3 \Rightarrow ^3Y_4 \Rightarrow ^4Y_4$$

(b)   discontinuous change: adaptation with reduced stress (buffered)

$$^1Y_1 \Rightarrow \quad ^2Y_2 \qquad \Rightarrow \quad ^3Y_3 \quad \Rightarrow \quad ^4Y_4$$

(c)   slow continuous change: adaptation "without" stress

FIG. 3.

State change walks (heavy lines with arrows) provoked by the environmental change $E_1 \rightarrow E_4$ occuring by three different modes:

  (a)   A sudden change for which the stressor is $\Delta E = E_4 - E_1$ and the corresponding stress intensity is $^1Y_1 - ^1Y_4$.

  (b)   A stepwise (discontinuous) change for which the stressor is applied as a sequence of doses, $E_2 - E_1$, $E_3 - E_2$ and $E_4 - E_3$, and the corresponding stress intensities are, $^1Y_1 - ^1Y_2$, $^2Y_2 - ^2Y_3$ and $^3Y_3 - ^3Y_4$.

  (c)   A continuous change proceeding very slowly so that the stressor is applied in infinitesimally small doses. The state change walk is the optimal walk.

Y is a system parameter expressing its actual performance and E an environmental factor. The values of Y are denoted as ^nY_m to indicate that the system is at a state adapted to an environmental factor E_n and exposed to an environmental factor E_m. Each of the four curves $^nY = f(E)$ (light lines) expresses the dependence of Y on E, within the certain adapted state (i.e. the state adapted to E_n). Open symbols correspond to optimality (n = m) and closed symbols to suboptimality (n $\neq$ m).
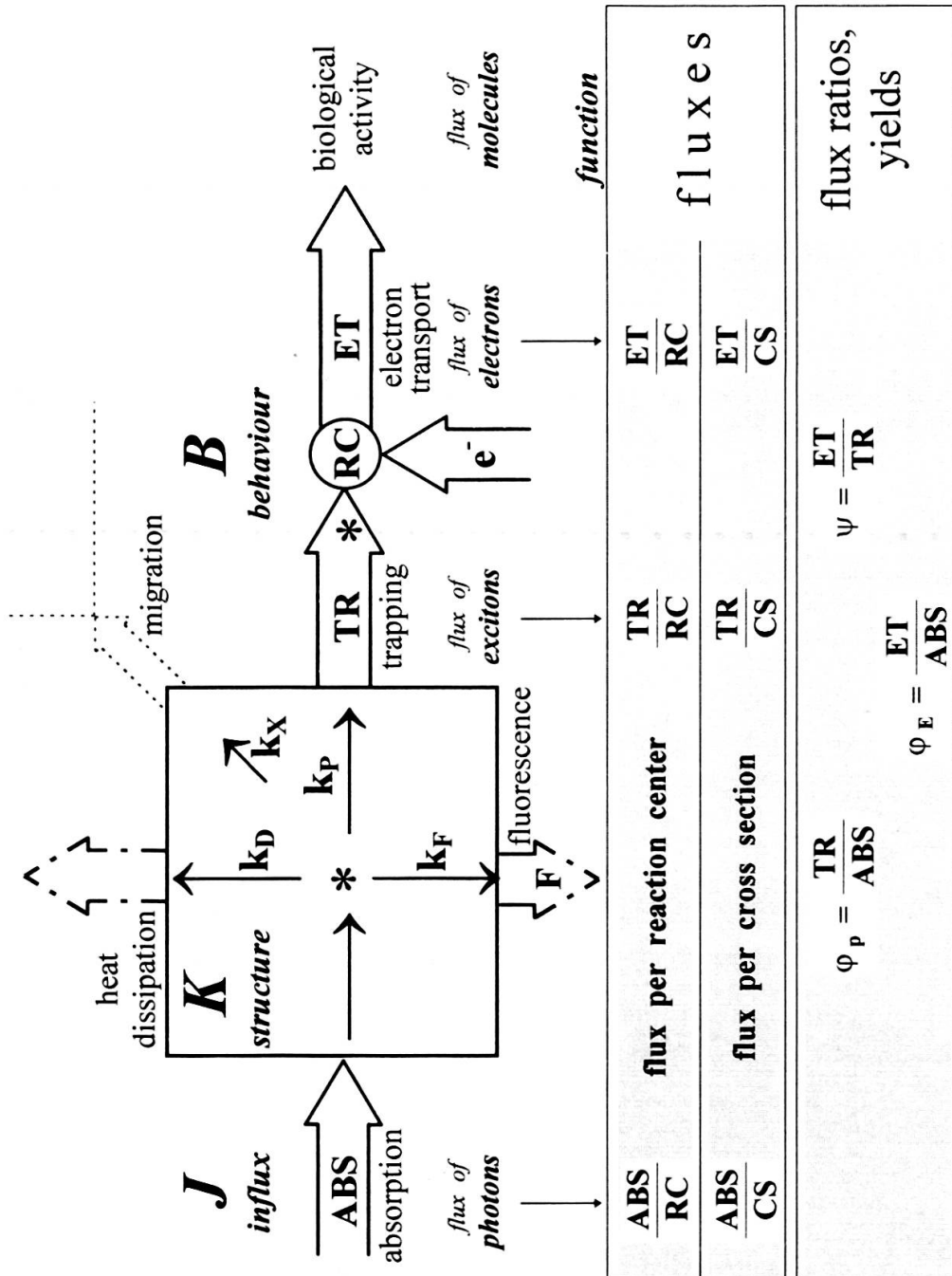
FIG. 4.

Photosystem II presented as an open system. The energy conservation, from the absorption flux **ABS** (flux of photons), to the trapping flux **TR** (flux of excitons), to electron transport **ET** (the flux of electrons) and, finally, to the biological activity (flux of molecules) is illustrated, as well as the deexcitation towards heat, fluorescence and exciton migration (spill-over and grouping). The deexcitation processes are also denoted by their rate constants: k_P (for photochemistry), k_D (for heat dissipation), k_F (for fluorescence) and k_X (for any energy migration). The correspondence with the terms of the JKB-trilogy is also indicated. The function of the system is presented by a constellation of expressions for energy fluxes - both per RC and per CS - and for flux ratios or yields, linked with the schematic presentation of the open system.
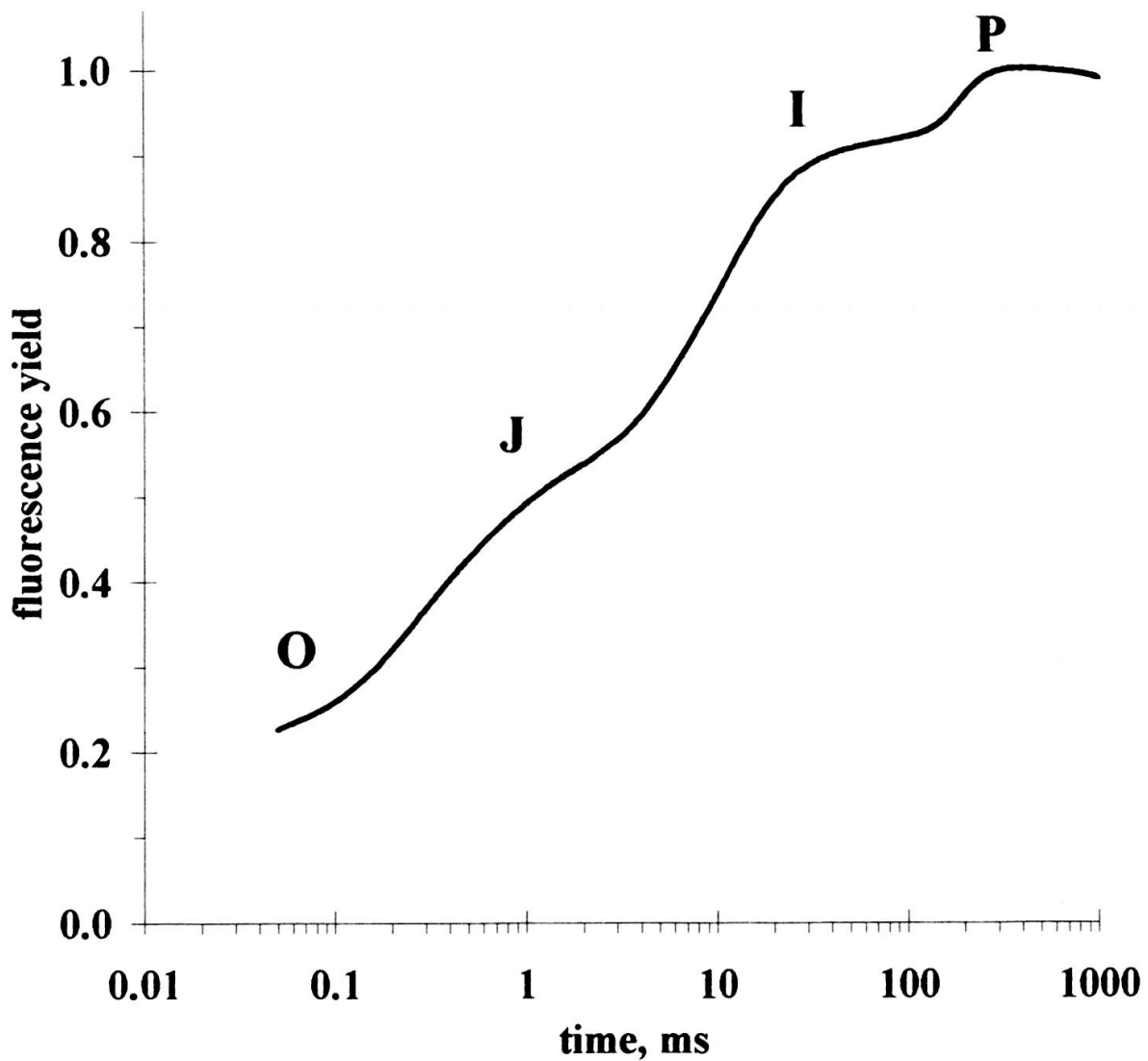
FIG. 5.

A typical **O-J-I-P** fluorescence transient induced by saturating illumunation, plotted on a logarithmic time scale. The point **O**, taken at 50 μs after the onset of illumunation, is considered as the initial point of the transient and the point **P**, at the maximum, as the end point of this fast phase. Between them, two more steps, denoted as **J** (at 2 ms) and **I** (at 30 ms), are clearly revealed.

$$k_N \qquad\qquad = I_{exc} \cdot k_F \cdot (1/F_M)$$
$$k_N + k_P \qquad = I_{exc} \cdot k_F \cdot (1/F_0)$$
$$k_P \qquad\qquad = I_{exc} \cdot k_F \cdot \{(1/F_0) - (1/F_M)\}$$

$$\varphi_{p0} \qquad\qquad = 1 - (F_0/F_M) \qquad\qquad = \quad k_P / (k_P + k_N)$$

$$1 - q_N \qquad\quad = (F_V/F_0) / (F_V/F_0)\text{dark} \qquad = \quad (k_P/k_N) / (k_P/k_N)\text{dark}$$
$$\text{where} \quad F_V = F_M - F_0$$

FIG. 6.

Expressions relating the conformational parameters with the experimental signals at the extrema of the fluorescence transient, i.e. at O and M (highest possible level of P). The conformational parameters are, the nonphotochemical deexcitation rate constant k_N and the photochemical rate constant k_P. Their link to φ_{p0}, the maximum photochemical quantum yield is also shown. Moreover, q_N, the so-called index for non-photochemical quenching is expressed through these parameters.
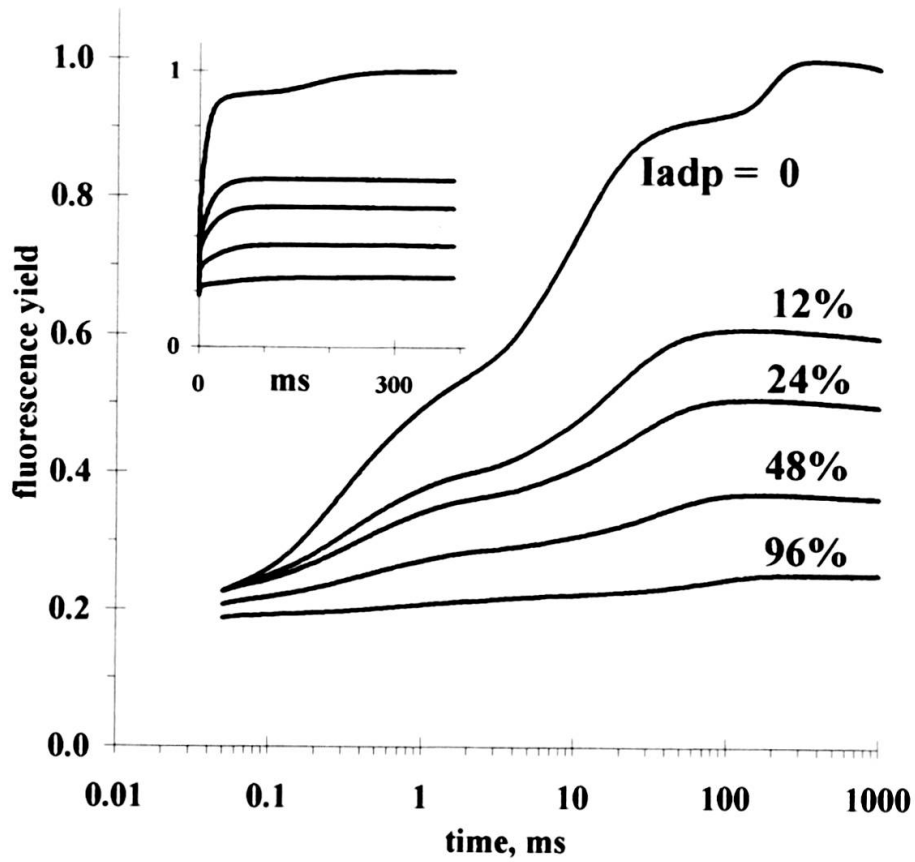
FIG. 7.

The **O-J-I-P** fluorescence transient at saturating I_{exc} (=96% of 600 Wm^{-2}) in leaves at different adapted states, on a logarithmic and a linear (insert) time scale. The adapted states are denoted by the corresponding I_{adp} (expressed as % of the I_{max} = 600 Wm^{-2}). The fluorescence yield for all states is expressed as a fraction of the value of F_P in dark adapted leaves.
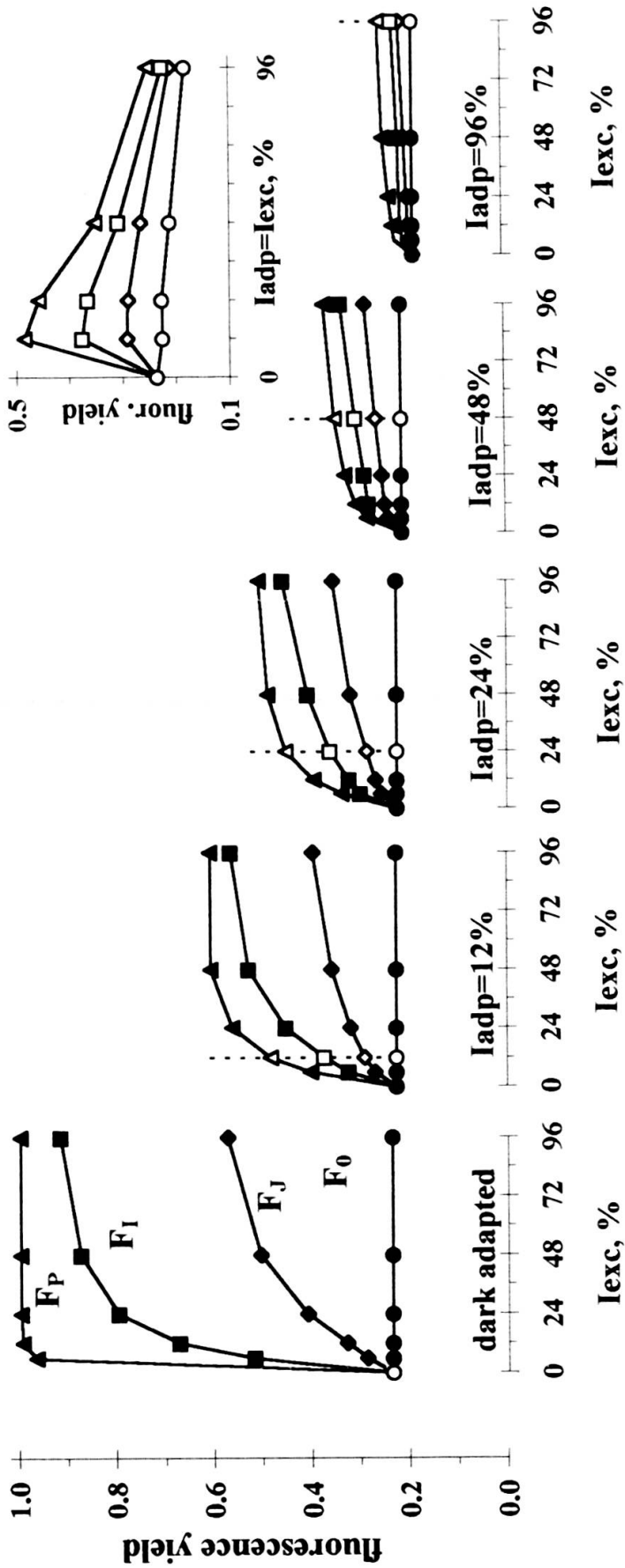
FIG. 8.

The fluorescence yield at the characteristic points of the fluorescence transients, as a function of I_{exc} for different adapted states (denoted by the corresponding I_{adp}, in % of the $I_{max} = 600$ Wm^{-2}). F_0 : at 50 μs, F_J : at 2 ms, F_I : at 30 ms, F_P : the maximal measured yield. The fluorescence yield for all states is expressed as a fraction of the value of F_P in dark adapted leaves. The open symbols refer to the non stressed conditions, i.e. to the conditions when $I_{exc}=I_{adp}$. Their dependence on this common value of the light intensity is shown in the insert.
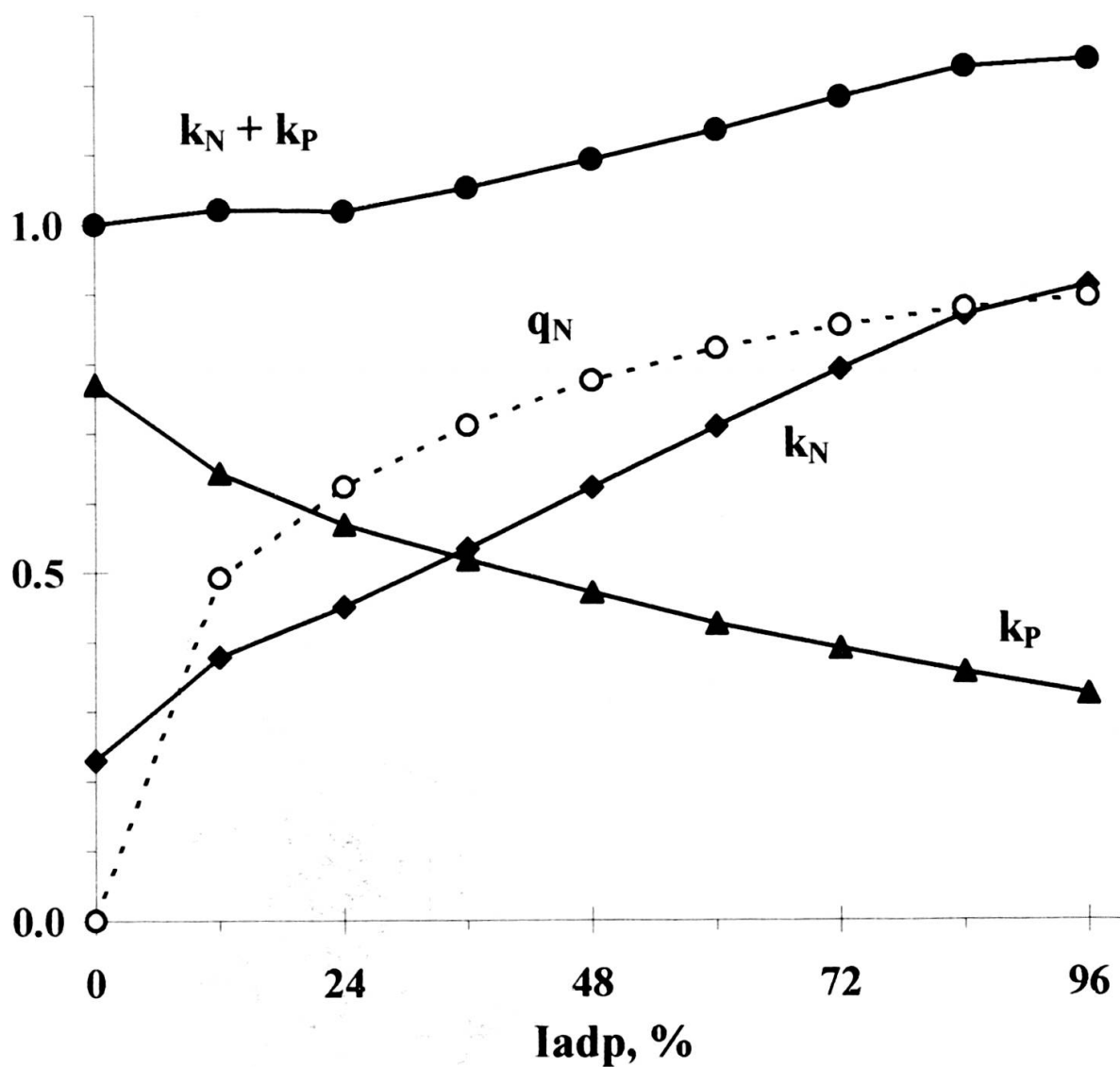
FIG. 9.

The dependence of conformational constants (in arbitrary units) on the adaptation light intensity I_{adp} (expressed as % of the $I_{max} = 600$ Wm^{-2}). k_P : the photochemical deexcitation rate constant; k_N : the nonphotochemical deexcitation rate constant. q_N , the so-called index for nonphotochemical quenching, is also shown for comparison.
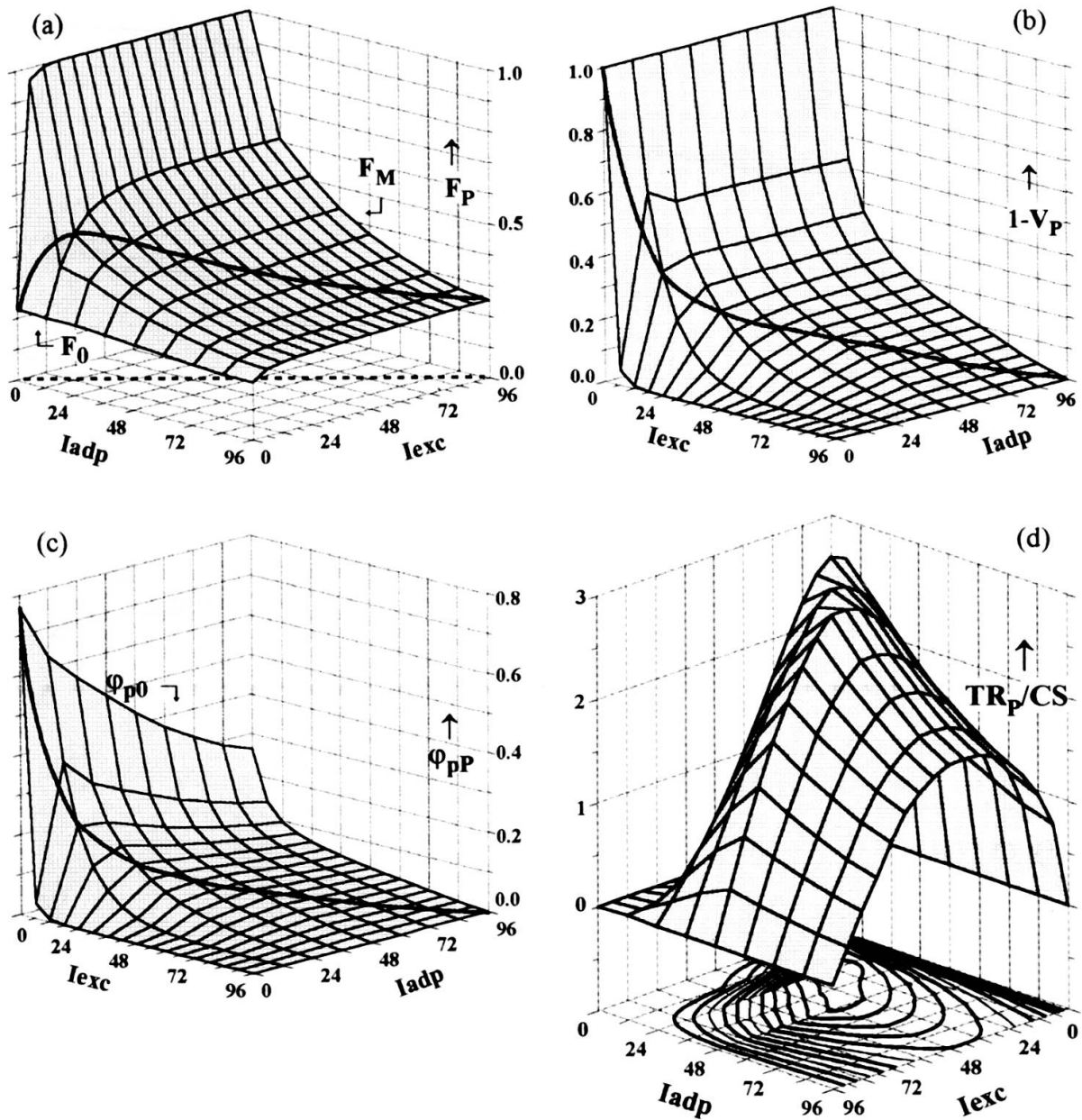
FIG. 10.

A 3-dimensional presentation of the dynamics of empirical and functional parameters at **P** (the stationary state) versus the adaptation (I_{adp}) and the excitation (I_{exc}) light intensity. (a) F_P : the fluorescence behaviour; (b) 1-V_P : where V_P is the relative variable fluorescence; (c) φ_{pP} : the yield or the energetic flux ratio; (d) TR_P/CS: the trapping flux per cross section. The vertical cut at $I_{exc}=I_{adp}$ (heavy line) reveals the transition function from darkness to high light intensity under steady state conditions and corresponds to the optimum state change walk.

$$V_P \qquad = (F_P - F_0) / (F_M - F_0)$$

$$\varphi_{p0} \qquad = 1 - (F_0/F_M)$$

$$\varphi_{pP} \qquad = 1 - (F_P/F_M) \qquad = \varphi_{p0} \cdot (1-V_P)$$

$$TR_P/CS \qquad = \varphi_{pP} \cdot I_{exc} \qquad = \varphi_{p0} \cdot (1-V_P) \cdot I_{exc}$$

FIG. 11.

Expressions relating the selected parameters of Fig. 10 with the experimental signal F_P (P being the stationary state revealed by the achievement of maximum fluorescence yield under the experimental conditions; maximum fraction of closed RCs, i.e. maximum B) and the experimental signals F_0 and F_M at the extrema of the fluorescence transient (F_0 being the initial fluorescence yield and F_M the highest possible level of **P**, achieved by a saturating light intensity; maximum possible fraction of closed RCs, i.e. B=1). The parameters are: V_P: the relative variable fluorescence, φ_{pP}: the yield or the energetic flux ratio; TR_P/CS: the trapping flux per cross section (all at the stationary state **P**).

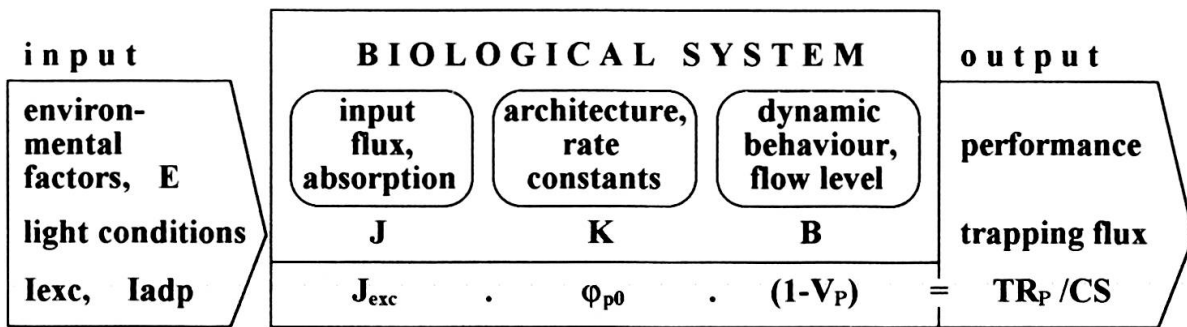| input	BIOLOGICAL SYSTEM			output
environ-mental factors, E	input flux, absorption	architecture, rate constants	dynamic behaviour, flow level	performance
light conditions	J	K	B	trapping flux
Iexc, Iadp	J_{exc} .	φ_{p0} .	$(1-V_P)$ =	TR_P /CS

FIG. 12.

The **JKB**-trilogy, by which any biological system can be approached, is specified in a schematic presentation for photosystem II. J_{exc}, the flux actually absorbed and utilised for excitation per cross section, is the **J**-term of the trilogy; φ_{p0}, the flux ratio, is entirely defined by the constellation of all deexcitation rate constants (Fig. 6) and can, therefore, represent the **K**-term; $1-V_P$, being an indicator of the flow level, corresponds to the behaviour of the system, i.e. to the **B**-term; TR_P /CS is an expression of the actual performance of the system.

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