

1 Environmental Signal Processing and Adaptation

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1.1 Introduction

The past 20 years have witnessed an explosion of new directions and perspectives in ecophysiology. These developments had, and continue to have, a profound influence on our understanding of animal and plant physiology, their life history, and how they match environmental constraints. What is ecophysiology? Depending upon the views of researchers and the diversity of their study areas, it may also be called physiological ecology, ecological physiology, environmental physiology, or even evolutionary physiology. These different names simply reflect the different approaches, whether one tries to understand how an animal has adapted to its environment, or how variations in physiology may affect the distribution of animals and plants in space and time. The approaches are not fundamentally different, since they all try to understand the mechanisms underlying distribution and fitness in animals and plants.

The focus of this book is on nongenetic adaptation and the analysis of proximate mechanisms of adaptation. What does this mean? All animals and plants are subject to short or long-term changes in their environment, like temperature, photoperiod, light intensity, or changing interactions with other organisms. They can only persist if they are able to cope with these changes in the environment, i.e., if they can adapt to changes in the environment. This adaptation requires that changes in the physical or organic environment are not only a load, but are also detected and responded by adequate adjustments of physiological functions. Changes in the environment are recognized as signals, which are processed and conveyed into a physiological response. The perception of environmental signals, their processing and control of biochemical, physiological, and behavioral responses was the integrated approach of 12 research groups at Marburg university, which outline their concepts and results in the present book.

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1.2 Acclimation and Adaptation

In the literature, these terms are often used as synonyms, sometimes causing confusion to the reader. Acclimation is defined as the adjustment of physiological capacities of individual organisms to changes in the environment, like cold, heat, bright light, etc. Acclimation improves fitness under these new conditions, and may be reversible. An acclimated individual is adapted to the new environment, and therefore the ability for this response is considered an adaptation. However, adaptation is also used for the evolution of physiological functions, i.e. the modification of genes which alter physiological functions, and genetically adapt an animal or plant to its environment. To discriminate between both meanings of adaptation, the latter can be assigned as genetic adaptation or evolutionary adaptation of species, in contrast to nongenetic adaptation or acclimation, describing the physiological adjustments of individual plants and animals to changes in the environment. However, the ability to acclimate is not an innate property of physiological functions, but was itself the result of genetic adaptation during evolution: for example seasonal acclimation of animals has evolved as an adaptation to seasonal cold load, or diurnal acclimation of plant photosynthesis has evolved as an adaptation to diurnal changes in light intensity and light quality. As soon as we analyze the biochemical or physiological mechanisms of acclimation we inevitably view this nongenetic adaptation as a genetic adaptation, and the discrimination between genetic and non-genetic adaptation may only be maintained when we restrict the term genetic adaptation to the study of evolutionary processes underlying acclimation.

1.3 Biological and Physical Signals for Plants

Seven chapters in this Volume deal with biological and physical signals for plants. The symbiotic signal exchange between bacteria and fungi as microsymbionts and higher plants as macrosymbionts is the combined aspect in the first three essays. Light adaptation, light harvesting, and light inhibition are the combining topics of the following four chapters. Symbiotic signal exchange also contributes to the basis of understanding the evolution of the eukaryotic cell, where chloroplasts and mitochondria have evolved from endosymbionts according to the generally accepted endosymbiotic theory of organelle evolution [1]. The molecular difference between friend and foe, symbiosis and defence, symbiont and pathogen is another interesting aspect of symbiotic signal exchange [2]. The comparison of the best-understood bacterial symbiosis (*Rhizobium/Bradyrhizobium* - legumes) [3, 4] and fungal symbioses (arbuscular mycorrhizas, ectomycorrhizas) [5] is also a combining aspect of the symbiotic signal exchange articles. The ecophysiology of symbiotic nitrogen fixation relates symbiotic interactions to plant nutrition and soil ecosystems [6].

1.4 Symbiotic Signal Exchange

The present knowledge in the ecochemistry of the rhizosphere and the signals produced by plants affecting microbes are summarized in by Phillips and Streit, Chapter 3. The most important compounds are flavonoids, affecting chemotactic activity, nod gene induction in rhizobia, spore germination, and hyphal growth in mycorrhizal fungi and regulation of other unknown genes. Phenolic compounds induce virulent genes and affect haustoria formation, amino acids and sugars have chemotactic effects besides being substrates for the energy metabolism of the microbial rhizosphere population. Antibiotic compounds in the rhizosphere include phenazines, phloroglucinols, phenylpyrroles, and pyrroles produced by *Pseudomonas* species, affecting phytopathogenic fungi in the rhizosphere. A very specific antibiotic is the peptide trifolitoxin produced by some strains of *Rhizobium*, affecting other *Rhizobium* strains as well as other rhizosphere bacteria. New results on very specific effects of vitamins in the rhizosphere have been found for biotin, increasing root colonization of alfalfa by *Sinorhizobium meliloti* several-fold. Even a very low concentration of 50 nmol biotin per plant is effective. On the other hand, a recombinant strain, overproducing biotin, was not more efficient in colonization of the plants. Biotin is also a cofactor for bicarbonate utilization; therefore it may also play an important role in the exogenous requirement of CO₂ for growth of *Rhizobium*, *Bradyrhizobium*, and *Sinorhizobium*. An almost completely unknown area is the function of nucleosides, accumulating in soils (up to $\mu\text{mol kg}^{-1}$ of soil).

Chapter 2 by Werner and Müller, *Communication and Efficiency in the Symbiotic Signal Exchange*, concentrates on several stages of the symbiotic interaction, producing a new plant organ, the legume nodule, and new cell organelles, the bacteroids, the nitrogen-fixing unit inside the infected cells. The alphabet A to Z was completely used to describe the identified nodulation genes (*nodA* to *nodZ*) involved in the biosynthesis of the nod factors and their transport inside the plant cells. A large number of laboratories in Europe, North America, and Australia were involved in this successful analysis for a new type of signal molecule, produced by microorganisms, affecting very specifically their host plants at rather low concentrations of 10^{-11} M, by root hair curling and branching, meristem induction, and nodule formation. Modification of the basic structure of the nod factors shows a unique variety of replacements of, e.g., a sulfate group by acetate, fucose, methylfucose, sulfo-methylfucose, acetyl-methylfucose, or arabinose and modification of the fatty acyl moiety with different chain length of the acyl group (C16 to C20) and also different placements of unsaturation.

More than ten different fatty acids have been identified in nod factors. Nod factors are produced in such a variety that they can be compared with safety keys with a small or a large number of specific edges. To understand the formation of infected cells inhabited by up to 10000 bacteroids in one infected cell in soybean, the involvement of signal peptidases is a major contribution. The *sipS* and *sipF* operons have been cloned and sequenced and the phenotypes of the specific muta-

tion described. A specific low expression of the new noduline 53 in the symbiosome membrane was established with these mutants.

The specific morphology and cytology in a fungal – plant interaction is summarized by Weber, concentrating on the endomycorrhizas in the Gentianales. Besides the general *Arum* type in the Asclepiadaceae, in the families Loganiaceae, Gentianaceae, and Rubiaceae all species studied had VAM structures of the *Paris* type with the following characteristics: the development of winding hyphae with a coil-like shape, the development of lumpy types of hyphae, and the lack of intercellular running hyphae within the root cortex. The molecular basis of these differences in the host plant reactions to the same species of microsymbiont is unknown.

1.5 Light Adaptation in Plants

Different groups of algae are the organisms used to study light adaptation, light harvesting and light inhibition. The detailed and comprehensive elucidation of the structure of hemidiskoidal and hemiellipsoidal phycobilisomes is in the center of the contribution by Wehrmeyer (Chap. 6). Very interesting differences between cyanobacteria, red algae and cryptophytes are described. Phycobiliproteins may represent up to 50% of the cellular protein in cyanobacteria, indicating their important role in adaptation to changes of environmental situations. In the red alga *Rhodella violacea*, the phycobilisome number changes from about 1000 PBS μm^{-2} under red light to about 600 under green light. Cryptophytes are an especially interesting group of algae, since they are the result of a secondary endocytobiosis. The cryptomonad biliproteins have a highly conserved amino acid sequence and an 80% identity with the rhodophytan PE subunits. Cryptophytes have a unique light-harvesting system with chlorophyll a/c antennae as well as extrinsic phycobiliprotein aggregates. In contrast to cyanobacteria and red algae, cryptomonads contain only one single type of biliprotein, phycoerythrin or phycocyanin.

The adaptation of the photosynthetic apparatus in green algae is summarized in the contribution by Senger, Humbeck, and Schiller (Chap. 5). They compare the results obtained with *Scenedesmus obliquus*, also with other green algae and with aquatic higher plants. Major results were achieved for the functions of carotenoids during adaptation by using several pigment mutants of *Scenedesmus obliquus*. The expression of the *cab* gene and the characterization of the different photoreceptors involved are described in detail in the contribution. The short-term and a long-term adaptation of the photosynthetic electron transport chain and the cytological involvement of antennae were also analyzed in detail. The cooperation of this group with the previous project (Wehrmeyer) demonstrates the cooperation within the Sonderforschungsbereich in Marburg.

The marine environment and ecosystem is the habitat of the seaweeds used in the studies by Hanelt and Nultsch (Chap. 8) on photoinhibition. Photoinhibition occurs in organisms exposed to irradiances exceeding the light energy requirement of photosynthesis. The basis of dynamic photoinhibition, chronic photoinhibition, and photodamage are described in detail. The seaweeds used in this study include

the brown algae *Dictyota dichotoma*, *Halopteris scoparia*, *Alaria esculenta*, and *Fucus serratus* and the red algae *Polyneura hilliae*, *Chondrus crispus*, *Delesseria sanguinea*, *Membranoptera alata*, *Phycodrys rubens*, and *Phyllophora truncata*. This is an important aspect of ecophysiology that not only one specific model organism is used but a more representative number of species for a certain habitat. It is demonstrated that the main target of photoinhibition is in photosystem II. Recovery from photoinhibition is species-dependent and the incident radiation must be reduced between 30 and 70%. An ecologically very important result is the demonstration that photoinhibition affects zonation of the algae on the shore. An important aspect of adaptation is also the capability, especially in brown algae, to displace their chromatophores from the low- to the high-intensity arrangement. A major conclusion from this study is that photoinhibition of photosynthesis is important for the survival of macrophytic algae in the natural environment.

1.6 Thioredoxins

The specific functions of thioredoxins in adaptation of plant metabolism to light and other environmental signals is the central theme of the contribution by Follmann and Häberlein (Chap. 7). They established a complete thioredoxin profile in the green alga *Scenedesmus obliquus* and in a higher plant, the soybean (*Glycine max*). Thioredoxins and light control and coordinate carbon, nitrogen, and also sulfur assimilation in chloroplasts. They participate in regulating ATP synthesis and NADPH. They affect enzymes of chlorophyll biosynthesis and enzymes of the carbon cycle, but not Rubisco. Especially important was the finding that the ferredoxin-glutamate synthase is a thioredoxin-dependent enzyme. In the algae *Chlamydomonas reinhardtii* and *Scenedesmus obliquus* four different thioredoxin genes have been found, whereas in higher plants such as corn, soybean, and spinach, six different genes were identified. This is further evidence that only the study of a number of different organisms leads to a complete and comprehensive understanding of biological diversity on a molecular basis.

1.7 Vibratory Signal Processing in Insects

Some insects, like crickets and cicada, use elaborate acoustic communication systems. The generation and perception of auditory signals for behavioral responses in insects is well documented. However, evidence has accumulated that their mechanoreceptors are also capable of detecting low-frequency vibration signals. Bushcrickets may transmit vibration signals to the substrate, e.g., branches, leaves or even soil; the signals may travel several decimeters in the substrate and are then sensed by another individual. The sensory organs for vibration signals are localized in the cricket legs, the campaniform sensillae, which are distributed in clusters in the cuticle of the tibia of all six legs. It was analyzed how



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