

PREFACE

Symbiosis refers to the biological interaction between two organisms or species, living in close association. In this book, the authors present current research in the study of the evolution, biology and ecological effects of symbiosis. Topics discussed include the evolution of arbuscular mycorrhiza; legume properties and symbiosis; sea anemones and hermit crab symbiosis in temperate seas; the agronomic and ecological importance between legumes and rhizobia; the behavioral, physiological and ecological effects of organisms in symbiotic associations; and a neuronal model with symbiotic interactions.

Mycorrhizas are universally distributed fungus-plant (root), mutualistic symbioses known to endow plants with an enhanced capacity to support environmental stresses. Arbuscular mycorrhizal (AM) associations are the most widespread mycorrhizal type formed by 70-80% of land plant species. The AM fungi, integrated in the phylum Glomeromycota, are ubiquitous microscopic soil-borne fungi which establish symbiosis with the plant by colonizing the root cortex without eliciting any significant defence reaction from the host plant. Evidences from fossil records, paleobotanical data and molecular approaches indicate that the origin and divergence of AM fungi date back more than 500 million years. Actually, AM associations evolved as a symbiosis highly specialized to facilitate plant adaptation to the primitive harsh terrestrial environment, being commonly accepted that AM fungi played a crucial role in land colonisation by plants. AM fungi colonize the root cortex and develop an external mycelium which acts as an extension of the root system and increases the uptake of mineral nutrients. In addition AM fungi enhance plant performance through an increased resistance/tolerance to diverse types of stress either biotic (pathogen attack), or abiotic (drought, salinity, contamination by heavy metals or organic pollutants, etc.). The cellular and molecular dynamics regulating AM formation and functioning are currently being elucidated. In Chapter 1, particular emphasis will be placed on discussing topics related to the exchange of signal molecules between symbionts during AM development, the plant symbiotic genes essential for the intracellular accommodation of AM fungi, the functional processes involved in the coordinated nutrient exchange between symbionts, and on the physiological and molecular basis for stress alleviation. The ecological impact of AM symbioses is based on their recognized effects at affecting rates and patterns of nutrient cycling in agro-ecosystems, thereby helping plant development in nutrient deficient soils, their role at enhancing plant performance through an increased resistance to diverse types of stress either biotic or abiotic, and at improving soil quality through the formation of stable aggregates. Strategic and applied research has demonstrated that AM fungi can be managed to help sustainable environmentally-friendly agro-biotechnological practices.

Chapter 2 aspires to summarize the major advancements in the experimental study and understanding of the internal regulation of the intensity of rhizobial symbiosis. This kind of symbiosis takes place in the roots of predominantly legume plants in the form of specialized organs, root nodules, that are colonized by the soil nodule bacteria (rhizobia). Although the bacterial microsymbionts belong to several taxonomic groups, they share the ability of initiating root nodule development and fixation of atmospheric dinitrogen, which is subsequently utilized by the host plant. The latter feature predetermines the economic importance of rhizobial symbiosis and of the regulation of its intensity. While the symbiotic nodule induction is mediated by highly specific bacterial lipochitooligosaccharides, called Nod factors, further regulation of plant response is strictly controlled by plant endogenous mechanisms. Surprisingly, the major regulatory circuit includes systemic signaling from the root to the shoot and backwards. The nature of the involved molecules has been unknown until recently, except for the shoot-acting protein HARI, described in 2003, and its homologs. Starting from 2008, a number of additional shoot-acting or root-acting regulatory mutants have been isolated. Their ongoing characterization has identified a series of new genes and products involved in the systemic signal generation, transduction and perception. Genomic approach allowed to identify low-molecular weight peptides of the CLE family as symbiotic signal messengers. The new experimental data enable a preliminary reconstruction of the systemic circuit and prediction of the nature of yet unknown components. A special interest represents the mechanism by which the inhibitory signal of ambient nitrate is integrated into the symbiotic circuit.

As explained in Chapter 3, improved nitrogen (N) management is needed to optimize economic returns to farmers and minimize environmental concerns associated with N use. Symbiotically N₂ fixed is of particular significance in sustainable agriculture as it allows reducing the use of chemical N in the production of field crops. The legume-bacteria symbiosis is the most important N₂ fixing system. This relationship is between bacteria collectively called *Rhizobium* and annual or perennial leguminous plants. In general, the rhizobia infect the plant via the root hair and invade the tissues. The cells are infected intracellularly, divided, and enlarged to produce the characteristic nodules (determinate or indeterminate). The importance of this relationship relies in the ability of the rhizobia to fix (reduce) the atmospheric N₂ to the host-plant, which in turn provides soluble carbohydrates to the microorganisms. Nitrogen fixation depends on legume performance, environmental conditions, soil nutrients availability, contaminants, bacteria abundance and diversity in soil, and bacteria specificity and infectivity for the legume. Under favourable conditions, legumes fix more than 50% of plant N.

Symbiosis, according to its initial meaning, refers to the biological interaction between two organisms living in close association. However, this definition is rather controversial, with the term being often used generically, since the outcome can vary across a continuum from negative to positive interactions. Symbiosis is a widespread phenomenon in temperate marine communities, and the association between sea anemones and hermit crabs belongs to the most common cases, being a familiar example of mutualism. In these latter specific cases of interactions gastropod shells are involved as prerequisite, since they provide both refuge for hermit crabs and substratum for the settlement of sea anemones; thus, shell resource availability is crucial for the establishment of this particular type of symbiosis. Within this context Chapter 4 aims to integrate the results of various studies to provide a general review about the symbiotic interactions of sea anemones and hermit crabs in temperate seas,

addressing the following issues: (1) clarify the relevant terminology, which is differently interpreted by various authors; (2) provide a general description of the sea anemone - hermit crab association, as most studies examine separately the species involved and not the symbiosis as a whole; (3) assess the diversity and distribution of sea anemone - hermit crab associations in temperate seas, also incorporating gastropod shells and their availability, which although crucial, has been only little investigated; (4) address the behavioural patterns of both symbionts for the establishment of the symbiosis, including as well the behavioural plasticity of hermit crab related to shell resource utilization, and (5) report relevant information about co-evolution of the participant species, referring to the existing hypotheses on the evolution of the symbiosis, underlining its importance.

Legumes are able to fix nitrogen because of the bacterial symbionts (rhizobia) that inhabit nodules on their roots. The amount of ammonia produced by rhizobial fixation of nitrogen rivals that of the world's entire fertilizer industry. Consequently, this symbiotic relationship between legumes and rhizobia is of great agronomic and ecological importance.

Typical environmental stresses faced by the legume and their symbiotic partner may include, water stress, salinity and temperature and influence the survival in the soil.

In the Rhizobia-legume symbiosis, the host plant also influence rhizobial survival. In *Arachis hypogaea* rhizobia symbiosis is known that different abiotic stresses affect the viability, trehalose and membrane components content of rhizobia. Also, the attachment ability of peanut rhizobia is affected under abiotic stresses.

Chapter 5 addresses the idea that the rhizobia and the plants must be able to adapt to survive to the environmental conditions. Our hypothesis is that rhizobia survival in the soil environmental because they are able to modify fatty acid and phospholipid components of their membranes, as well as other molecules with important roles in stress tolerance.

As discussed in Chapter 6, the significance of coevolutionary adaptations by associated organisms at the cellular and molecular level has been the primary focus of much research in symbiology (e.g., endosymbiotic hypothesis for development of eukaryotes). Studies on the behavioral and physiological ecology of organisms involved in symbiotic associations have also demonstrated extraordinary examples of adaptation. These associations represent tremendous potential in demonstrating alternatives to competition as major evolutionary selective forces. Interactions vary tremendously within the commensalism, mutualism and parasitism subdivisions of symbiosis, and divergent examples will be discussed. For example, many organisms are limited by their anatomy to remove parasites and necrotic tissues, etc., and must rely on allogrooming by others. While terrestrial animals are usually better equipped for autogrooming, the "self-cleaning" problem is especially significant in marine environments where cohorts of animals switch from potential predators to symbiotic cleaning "clients." Organisms that possess significant, innate adaptations for protection are potentially attractive commensalistic or mutualistic hosts if a potential symbiont can inhibit or withstand the defensive mechanisms. Parasitism has also demonstrated bizarre behavioral outcomes, including examples where a larval form can "force" an intermediate host to alter its behavior to facilitate completion of the parasite's life history. Finally, the characteristics or phenotypes of many organisms are actually based on composite genotypes of the host and any significant symbionts.

More than 200 species of non-legume dicotyledonous plants, mostly trees and shrubs, belonging to eight different families and 24 genera can enter actinorhizal symbioses with the nitrogen-fixing actinomycete *Frankia*. Actinorhizal nodules arise from divisions occurring in

the pericycle and display a lateral root structure with a central vascular system and infected cells in the expanded cortex. Recently, the development of genomics both in *Frankia* and in actinorhizal plants, together with the possibility to obtain transgenic actinorhizal plants following *Agrobacterium* gene transfer, offered valuable tools to achieve significant progress in the understanding of actinorhizal symbiosis. Molecular data indicates that, like in legumes, actinorhizal symbiosis is a highly controlled process, involving plant signals perceived by the actinomycete and specific *Frankia* factors perceived by plant roots, that activates a symbiotic signalling pathway. In Chapter 7, current knowledge on the actinorhizal symbiosis will be discussed in the context of plant root endosymbioses evolution.

As explained in Chapter 8, improved nitrogen (N) management is needed to optimize economic returns to farmers and minimize environmental concerns associated with the N use. Symbiotically N₂ fixed is of particular significance in sustainable agriculture as it allows reducing the use of chemical N in the production of field crops. Intercropping or crop rotation including legumes promises a more sustainable plant production in many agricultural systems through the N transfer and N release from legume residue. Sharing of N sources between the intercropped N₂ fixing and non-fixing plants contribute to a better overall N use. In a crop rotation, the final contribution of fixed N₂ to the soil depends upon the crop N balance, environmental conditions and agricultural practices.

In Chapter 9 the authors investigate various ecosystems containing always a symbiotic pair. In the first model, the latter is subject to the action of a predator. In the second system, the mutualistic association at the trophic level is located above a common prey population. In the third model a three level food chain is investigated, with the symbiotic populations constituting the intermediate trophic level. These are situations that can well arise in nature.

Finally, the authors make considerations on a symbiotic system in which a population X predaes on another population Z; a third population Y lives in symbiosis with X; finally Z predaes on Y. Such an association is rather difficult to find in nature, but an interpretation of it could come from the world of finance, in which biological "populations" are substituted by corporations. At times they interact among each other in search for synergies, but at the same time it may occur that part of these associations compete with each other in other fields, giving rise to rather intricate situations as the one described above.

In general, the behavior of large and complex aggregates of elementary components can not be understood nor extrapolated from the properties of a few components. The brain is a good example of this type of networked systems where some patterns of behavior are observed independently of the topology and of the number of coupled units. Following this insight, in Chapter 10 the authors have studied the dynamics of different aggregates of logistic maps according to a particular *symbiotic* coupling scheme that imitates the neuronal excitation coupling. All these aggregates show some common dynamical properties, concretely a bistable behavior that is reported here with a certain detail. Thus, the qualitative relationship with neural systems is suggested through a naive model of many of such networked logistic maps whose behavior mimics the wakingsleeping bistability displayed by brain systems. Due to its relevance, some regions of multistability are determined and sketched for all these logistic models.