Symbiotic Nitrogen Fixation in Actinomycete-Nodulated Plants. Preface
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SYMBIOTIC NITROGEN FIXATION IN ACTINOMYCETE-NODULATED PLANTS

PREFACE

For forested ecosystems, fields, wetlands and dry sandy soils in disturbed sites in north- and south-temperate regions, symbiotic nitrogen fixation occurs in substantial amounts through the activities of a diverse group of woody dicots whose roots form nodules in response to invasion by soil bacteria belonging to the Actinomycetales.

This volume results from an informal meeting at the Harvard Forest in Petersham, Massachusetts, in April 1978, of about 35 scientists from the United States and Canada engaged in research on these plants and their symbionts. The participants represented a wide range of interests, including the microbiology of the soil bacteria, the physiology and biochemistry of the symbioses, the structure and function of the roots and nodules, and the activity and productivity of the host plants as components of specific ecosystems, including forested areas managed for pulp, timber, or biomass production. All of these subjects were discussed, and many of them form the basis for the papers published here. Other topics discussed at the meeting will lead to publications in the future.

Recognition of the common interests of the group assembled evolved from recent strides made in three areas. Through the stimulus of the International Biological Program (IBP) over the past decade and under the leadership of Professor G. Bond of the University of Glasgow, Scotland, serious efforts had been made to establish a worldwide accounting of the diverse groups of plants which possess symbiotic nitrogen-fixing capacity due to actinomycete-infection of their root systems. In the IBP volume in 1976, edited by P. S. Nutman (Cambridge University Press), Bond's tally showed that 160 species of woody dicots, belonging to 15 genera among seven families, make up a surprisingly diverse group which shows few common features other than susceptibility to infection by actinomycetes.

The significance of symbiotic nitrogen fixation by this assemblage of plants came with the recognition that these organisms by and large were capable of fixing atmospheric nitrogen at rates comparable to the legume-*Rhizobium* systems, measured on an individual fresh weight or dry weight basis using rate of ^{15}N-fixation or acetylene-reduction measurements or calculated from field data on a kilogram per hectare basis. For north- and south-temperate regions of the world, the fixation is of large magnitude and needs to be fully understood and appreciated more widely.

The second forward step in this field has been the recognition, especially by foresters, that these symbiotic associations can begin to be manipulated to the benefit of man. The major crop plants are trees, important for lumber, for pulp, and with modern technologies, for biomass and energy production. Reports included in this volume illustrate some of the favorable management practices already begun. Species of alder appear particularly favorable for interplanting with important crop trees. The actinomycete-nodulated plants provide not only for their own nitrogen needs by fixation but also adequately feed the plants with which they are intercropped. Understanding of the importance of these associations has been accelerated by the increasing worldwide cost and shortage of energy for chemical fertilizers. Developing and developed countries are equally interested in the application of these ideas to forestry management. The direct benefits are through leaf fall and subsequent assimilation of fixed nitrogen; responses of associated plants are rapid; i.e., a few years suffice for measurable responses. Such stimulation of growth rates and productivity can be observed in diverse dual plantings: red alder–Douglas-fir, European alder–poplar, autumn olive–black walnut, and others. In the tropics, plantations of *Eucalyptus-Casuarina* may be excellent combinations for interplantings in which the nitrogen-fixing capacity of the actinomycete-nodulated plant can be harnessed to the needs of both species directed toward rapid biomass production. These same associations show great promise for use in recovery of disturbed lands, of lands distressed by mining operations, or those nearing destruction from poor land-management practices which, in the past, have allowed erosion or depauperization of the soils. Progress also is anticipated in combining these favorable associations with appropriate mycorrhizal fungi to alleviate problems of phosphate availability or other inorganic constituents.

The third and most recent development in this field has been the optimism brought to the possibility of management of the symbiotic associations by the successful isolation and partial characterization of the actinomycete partner in the symbiotic association. The *Comptonia* isolate growing in culture shows structural features observed in the endophyte in vivo—a filamentous bacterial mycelium, sporangia of distinctive size and shape producing spores of discrete character. Suspensions of the organism grown in culture can be applied to seedlings of appropriate hosts and predictable infection can be studied and prompt nodule initiation and formation assured. Root hair infection seems to be the common mode of entry from the soil stage of the actinomycete. By analogy to the *Rhizobium*-legume system, one can hope to select the most effective host-symbiont combinations for highest nitrogen-fixation rates and maximum productivity in the field.

Availability of the cultured organism and susceptible seedling hosts makes accessible more rigorously controlled physiological experimentation on the symbiosis itself, an area discussed but notably lacking in this published volume. Similarly, one can expect that biochemical studies will be facilitated, including isolation and characterization for comparative purposes of the nitrogenase enzyme, the mechanisms of oxygen protection within the nodule, and the relative efficiencies of the various associations. Thus, a major gap in this area of research can begin to be filled. Such comparisons of actinomycete- and *Rhizobium*-induced nodules should help to elucidate as well the basic requirements for symbiotic nitrogen fixation.

An exciting area that is briefly touched upon in several papers in this volume is the subject of cross-inoculation, i.e., the capacity of the actinomycete from one host to cause nodulation of another taxonomically different host. The study of cross-inoculations already has been pursued using suspensions prepared from ground-up nodules. With the availability of pure cultures of actinomycetes, the subject becomes much more rigorous and intriguing and may begin to open up our understanding of host susceptibilities, the nature of bacterial-host recognition, and the biochemical as well as morphological nature of the infection process itself. Thus, as reported in these pages, the actinomycete isolated from *Comptonia peregrina*, designated *Frankia* sp. CpI1, effectively nodulates its own host, also *Myrica gale*, *M. cerifera*, and *M. pensylvanica* within the same family and, in addition, *Alnus crispa*, *A. glutinosa*, *A. rugosa*, *A. rubra*, and probably other alders, all in a different family. The *Comptonia* isolate does not cause effective nodule formation on a number of host plants tested, including *Ceanothus americanus*, *Casuarina cunninghamiana*, and *Elaeagnus umbellata*, to name a few. What is the nature of this discrimination? More important, can we overcome the resistance of these host plants, and further, can we extend the capacity of these soil microorganisms to infect and nodulate other host plants, perhaps more directly important to man? This is a research subject which still lies in the future; yet one must be optimistic that actinomycete associations already so diverse can be broadened even further when we know somewhat more than we do now. The open-ended search for new actinomycete-nodulated plants goes on—the list is now nearing 170 species and continues to rise. Perhaps laboratory studies will make possible a dramatic rise and in directions of special importance to man. That is at least one of the incentives to pursue these associations with increasing intensity.

While several national and international meetings on N_2 fixation have been held in the recent past, no gathering of scientists has dealt specifically with the research problems of this specialized group of plants. There was at the meeting a sense among the participants of the genesis of a new and important field. A serious effort was made in informal discussions to devise a convenient designation for the field, one more positive than the much used but noninformative term "nonlegume." Among suggestions voiced at the meeting to replace the somewhat cumbersome title used for this volume were the following terms: "actinomycetorhizal," or a more abbreviated form "actinorhizal," or, to parallel the fungal counterpart, "actinomycorrhizal." Perhaps usage and the test of time will select from among these designations.

We have published below the entire program, together with the names and addresses of the participants at the meeting, to show the range of topics covered and to stimulate further interchange among scientists in this field.

The organizers of the conference and the participants are grateful to the Harvard Forest and to the Maria Moors Cabot Foundation for Botanical Research of Harvard University for serving as hosts. Special thanks are expressed to W. R. Bentley, manager of forestry research of Crown-Zellerbach, for his encouragement and support of this meeting of minds. Thanks are also expressed to the editors of the *Botanical Gazette* who were instrumental in arranging for the publication of these papers in a single special issue of this journal.

An international workshop of actinomycetorhizal research workers is planned for April 1979 at Corvallis, Oregon. Inquiries can be sent to Dr. J. C. Gordon, Department of Forest Science at Oregon State University.

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