Differentiation Patterns in Tigher Plants

edited by KRYSTYNA M. URBANSKA

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Foreword

The contemporary vigour of the plant biosystematics is amply illustrated by the fine collection of chapters that constitute the present volume. Despite premature accounts of its demise, the detailed experimental study of plant populations continues to attract outstanding scientists. Although the main preoccupation of biosystematics has shifted over the past 50 years from the properties of species and populations to features of the local breeding populations, deductions at all levels of biological organization, when based on experimental studies, continue to be made usefully. The steady growth of the International Organization of Plant Biosystematists (IOPB) itself provides but one measure of the vitality of the field, and the organization of this excellent symposium in Zurich by Krystyna Urbanska constitutes a second such measure.

Traditional biosystematic fields, such as the role of hybridization in plant evolution, the nature of the ecotype, the radiation of species on islands, and the evolution of weedy and colonizing species, are well represented in this book and receive a great deal of attention from biosystematists. On the other hand, new tools such as the comparative analysis of nucleic acids both in the nucleus and in mitochondria and chloroplasts and the investigation of isozymes, are producing new and exciting results. The continued application of such tools, and of powerful mathematical methods of analysis, spurred by the application of computers in a way unthinkable in the 1950s, will produce valuable results for many years to come.

The exploration of breeding systems in plants continues to be of great interest to plant biosystematists. In this connection, C. D. K. Cook's suggestion in this volume that the lack of sexual reproduction may constitute a price to be paid for ecological specialization is an interesting one, and consistent with much of our knowledge. The application of the methods of demography to the understanding of the population structure likewise offers great promise for increasing our understanding of plant evolution. Such an approach is illustrated in this book by the distinguished contribution of Schoichi Kawano and his colleagues.

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We are coming to understand all of the facets of plant growth and development better, and this understanding will have important applications in the more completed research of plant evolution. For example, the studies reported by Bruce Knox in this volume, like so much of his excellent work, are most informative about the function of pollen grains and stigmas and thus of incompatibility and the possibility of obtaining hybrids. The understanding of these processes will ultimately help us to assess the evolution of barriers to interspecific hybridization and consequently the functioning of plant species in nature.

In the present volume, about half of the chapters are devoted to what might be called the field of plant population biology. The vigorous and mutually beneficial hybridization of this field with traditional plant biosystematics is nicely illustrated. It will be exciting to study the fruits of this hybrid in more detail at the next IOPB symposium in Japan in 1989.

Peter H. Raven Missouri Botanical Garden, St Louis, MO, U.S.A.

Preface

This volume is based on Invited Papers presented at the IOPB Symposium held in Zurich, Switzerland, 13–18 July, 1986. The Symposium was sponsored by the International Organization of Plant Biosystematists, the International Union of Biological Sciences, Swiss Academy of Science, and the Swiss Federal Institute of Technology, Zurich. The generous financial support of the two latter institutions is gratefully acknowledged.

We believe that a better knowledge of differentiation occurring over a wide range of scales and systems of biological organization will result in a more integrated approach to the problem of evolution in higher plants. The purpose of the Symposium was therefore to promote exchange of ideas and experiences between scientists representing various backgrounds and interests. This book is aimed at workers interested in the interface of plant ecology with genetics, demography, reproductive behaviour, etc. May the reader find the chapters that follow as stimulating as the Symposium participants have found the Invited Papers presented.

It is a pleasure to thank various staff members of the Geobotanical Institute, SFIT Zurich, and the Botanical Institute, University of Zurich, who provided assistance during the Symposium. I am also particularly grateful to Ms Susy Dreyer, Ms Anita Hegi, Ms Erica Wohlmann, Gaby Elmer, Marc Nicholls and Martin Schütz, who greatly helped with the preparation of this volume.

K. M. Urbanska Zurich, Switzerland

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Part I INTRODUCTION

Introductory Remarks

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The complex processes and patterns of differentiation in higher plants operate at *various levels*, from the molecular level of mutation to the biological level of adaptation (Grant, 1985). No particular level can be singled out as the most important.

Since evolution takes place in a continuum of populations through time, all evolutionary processes must, in the final analysis, take place at the population level (Sokal, 1978). The increased interest in plant population biology during the last decade (see e.g. Harper, 1977; Dirzo and Sarukhan, 1984; White, 1985) is undoubtedly influenced by this understanding. The question arises, however, whether the principles of modern population biology are sufficient to explain all evolutionary processes. Differentiation obviously occurs in *diverse biological systems*, and may thus be influenced by some system-specific properties, even if the principal biological rules governing plant life are the same everywhere. Spatial and temporal patterns of differentiation occurring within and among populations, communities, and ecosystems may thus relate to conditions particular to a given system, with historical factors representing an important element.

At the time being, the question stated above remains open, with more new information being required. Another problem is that some data on various systems are available, but remain scattered in the literature and have yet to be brought together.

The knowledge of *diverse aspects* of differentiation is also essential for an accurate assessment of evolutionary potential of a given development. Recent studies in this subject demonstrate that some long-standing beliefs need to be

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revised. For example, asexual reproduction does not preclude differentiation in some plants (see e.g. Urbanska, 1985; Landolt, 1986). Not only plant reproduction, but also other important aspects are being given increased attention and new insights are being obtained; among them are gene flow (see e.g. Loveless and Hamrick, 1984), phenotypic plasticity (see e.g. Bradshaw, 1974; Schlichting, 1986), or the niche problem (see e.g. Bazzaz, 1986). All these studies show that there is no clear separation between genetics, ecology, and studies in plant behaviour, and that approaches from diverse fields of plant life science urgently need to be integrated.

Our purpose in organizing this volume was to treat differentiation in higher plants in its diversity, the contributors having been selected accordingly. This book does not cover all possible aspects of differentiation as no single volume can do this; rather, it was intended to present some ideas and examples that might prove useful for future research. The first part of the book focuses on diverse levels and aspects of differentiation. The first two chapters are concerned with the genetic component of plant evolution; they discuss genome differentiation (Grant, Chapter 1), and genome transcription patterns in differentiation of gametes (Knox, Chapter 2). The subsequent chapters develop the theme of interplay between genetic and ecological factors for particular aspects of differentiation: gene flow (Hamrick, Chapter 3), variation in environmental parameters (Bazzaz and Sultan, Chapter 4), and phenotypic plasticity (Quinn, Chapter 5). The last chapter of Part II deals with natural hybridization, which does not merely represent a re-fusion of differentiated genomes, but often leads to a further differentiation (Stace, Chapter 6).

In Part III examples of differentiation in diverse biological systems are presented. Various patterns are shown in adjacent populations of a single species inhabiting two different environments (Vernet et al., Chapter 7), different species of the same family occurring in temperate woodland within a rather limited area (Kawano et al., Chapter 8), congeners on oceanic islands (Crawford et al., Chapter 9), and also in a single family of aquatic plants distributed all over the world (Landolt, Chapter 10). Species representing various families are discussed in chapters concerned with aquatic weeds (Cook, Chapter 11), and tropical woody plants (Ehrendorfer, Chapter 12). Finally, the whole vascular flora of a large Arctic region is dealt with (Murray, Chapter 13).

So far as I am aware, most of the material presented here is new and has not previously appeared in book form.

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