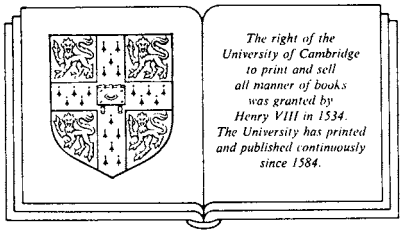
Nature as the laboratory

Darwinian plant ecology in the German Empire, 1880–1900

Eugene Cittadino



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Introduction

As the opening speaker at a special session of the Munich Academy of Sciences in 1898, plant morphologist Karl Goebel chose as his topic "On the Study and Interpretation of Adaptive Phenomena in Plants." He cited three reasons for the recent interest in adaptation among European botanists. To begin with, it seemed to Goebel that the study of the internal structure and development of plants had come to a standstill at the close of the nineteenth century. The really exciting discoveries lay in the past; there was little hope that in the near future researchers would unravel the mysteries of the composition and properties of protoplasm. He likened the situation to that of a mountain climber who views with despair the seemingly insurmountable peaks ahead of him and then suddenly realizes that there is much that is of interest in the maze of ridges and gorges that lie close at hand. Thus perceptive botanical adventurers had recently discovered a host of interesting problems having to do with the relationship of organic structure to the external world, problems that, unlike those dealing with the ultimate nature of the living material, admitted of possible solution. But this seemed a largely negative incentive for studying adaptation. Goebel then suggested two positive sources of stimulation. One was Darwinism; the other was the opening up of the tropics to serious botanical research. With the establishment of modern laboratory facilities, such as that at Buitenzorg, on the island of Java, European botanists could study living tropical plants in their natural setting; they no longer had to rely upon dried specimens or upon observations of plants living in the artificial environment of a greenhouse. The greater taxonomic diversity of tropical vegetation and the wide range of environmental conditions available in the tropics allowed them to investigate adaptive phenomena that were barely discernible in native European plants.[1]

In these brief remarks Goebel accurately characterized the essential features of a movement that had been developing since the early 1880s. Young German botanists trained within a well-established inductive laboratory tradition had ventured out of their laboratories (or rather had transferred their laborato-

ries, figuratively and in some cases literally, outdoors) and had made important contributions to Darwinian biology and to the not yet formalized science of plant ecology. During the early 1880s, the already prolific botanical literature in Germany was marked by an increase in the number of studies dealing with the relationship between the minutiae of internal structures and factors in the external environment of the plant, such as moisture, temperature, and light. This work increased in volume and sophistication during the 1880s and 1890s and rapidly came to include studies of vegetation found in exotic regions. When they gave it a specific name, the Germans usually called this new line of research "plant biology," to distinguish it from purely descriptive botany and from highly specialized, and less interpretive, studies in plant anatomy and physiology. Today this work would fall within the province of plant ecology, specifically autecology, or physiological plant ecology.[2]

Although Darwinism was doubtless a strong factor in the development of research into plant adaptation, Goebel could not have overemphasized the role played by experiences in exotic environments. Opportunities for German botanists to travel in the tropics and in other regions outside Europe were closely linked to imperialism in one form or another. Since the 1860s, the Academy of Sciences of Berlin (officially the Royal Prussian Academy of Sciences) had been sponsoring scientific expeditions to regions where Germans had commercial interests. The expeditions became more frequent after the mid-1880s, when Germany officially acquired "protectorates" in Africa and the East Indies. Ambitious young botanists could convince the Berlin Academy, or a similar regional scientific body, to help finance an excursion to the Egyptian desert or the American tropics, not to mention the new German territories in Africa. In addition, Dutch botanist Melchior Treub established his botanical research laboratory at Buitenzorg just a few years before Bismarck successfully negotiated with the British for control of nearby islands in Micronesia. Thereafter, a steady stream of German botanists paid visits to Treub's laboratory.

Treub would have had few German visitors, however, had it not been for the abundance in Germany of professionally trained botanists with sufficient laboratory experience to make good use of the facilities at Buitenzorg. Botanical programs in German universities had been turning out laboratory-trained botanists at a fairly steady rate since the 1850s. The difficulty of obtaining a permanent university appointment had not discouraged young men from pursuing advanced training in botany. Although established professors as well as *Privatdozents* made the trip to Treub's laboratory, younger botanists who did not have permanent appointments had the time, and the motivation, to make repeated and/or extended visits to the tropics. They could carry out research to help advance their budding academic careers while taking part in the general expansion of German interests beyond the national boundaries of the Reich.

I owe the title of this book to Ernst Stahl, one of these German researchers, who is alleged to have remarked on numerous occasions: "My laboratory is Nature."[3] In many ways, Stahl's background is typical of the botanists considered in this study. Trained by the preeminent plant morphologist and plant physiologist of his day – Anton de Bary and Julius Sachs, respectively – Stahl began his research career making minute investigations into isolated botanical phenomena and then gradually shifted his focus to the relationship between the plant and its environment. The subject of his research became neither plant anatomy nor plant physiology, but plant *adaptation.* Like the others, Stahl felt dissatisfied with the limitations imposed upon botanical inquiry by the narrow inductive laboratory tradition, and he wished to apply his thorough training within that tradition to problems concerning the living plant in its natural habitat.

How and why this interest in plant adaptation should have developed in Germany during the last two decades of the nineteenth century is the central theme of the present work. The approach that I follow is to build up a group portrait of the key figures in this movement, supplying background material where necessary and focusing in detail on some of the central motivations behind and implications of this research program. Although the time constraints are not intended to be strict, the years 1880–1900 represent, for all of the botanists concerned, the period of their most active research regarding plant adaptation. The central figures in this group – Gottlieb Haberlandt, Georg Volkens, Stahl, and A. F. W. Schimper – are relatively unknown even among biologists and historians of biology. The minor figures – Heinrich Schenck, Alexander Tschirch, Emil Heinricher, and Albrecht Zimmermann – are still more obscure. However, all of them were known, and some quite well known, among plant scientists within and outside Germany in the late nineteenth and early twentieth centuries, especially among the growing community of field-oriented botanists who were beginning to articulate the content and methodology of a formal science of plant ecology.

Plant ecology was the first of the various branches of ecological science to be pursued self-consciously, as a discipline in its own right. Animal ecology, limnology, marine ecology, population biology, and other ecological fields developed more or less independently and matured somewhat later than plant ecology. (The first serious glimmerings of a *general* science of ecology appeared only in the 1930s, and the active pursuit of a unified ecological science is largely a post-1960 phenomenon.) Because many of the early plant ecologists directed their attention to the plant community rather than the individual plant, and because the study of plant communities remained a dominant emphasis in plant ecology well into the twentieth century, both ecologists and historians of ecology have searched for the roots of plant ecology in nineteenth-century phytogeography and have ignored, until recently, the en-

vironmental emphasis of many of the anatomical/physiological studies in late-nineteenth-century German botany. The attempts by nineteenth-century phytogeographers to relate patterns in vegetation cover to the nature of the physical environment certainly have a central place in the history of plant ecology. However, plant ecology has always endeavored to do more than simply associate vegetation patterns with particular environments; since its beginnings, the science has been preoccupied as well with the *causes* of pattern and change in plant communities. Danish botanist Eugenius Warming, a pioneer community ecologist and one of the principal founders of formal plant ecology, made this point quite clearly in one of the first textbooks in the new field. Warming stated that, in addition to identifying natural plant communities and determining the general physiognomy of vegetation in particular regions, ecology seeks "to investigate the problems concerning the economy of plants, the demands that they make on their environment, and the means that they employ to utilize the surrounding conditions and to adapt their external and internal structure and general form for that purpose."[4] As such, plant ecology has had to rely on the kinds of detailed, physiologically oriented studies relating habitat factors to plant structure that characterize the work of the German botanists under consideration here. Despite the descriptive nature of many of the early formal contributions to plant ecology, both European and American plant ecologists recognized a debt to these German ecophysiological botanists and continued to insist on the close connection between plant ecology and physiology.

For their part, however, the Germans who initiated plant adaptation studies in the late nineteenth century were not seeking to found a new scientific discipline. They were seeking only to broaden the scope of botanical science by redirecting the focus to the plant in its natural surroundings. Their botanical training had a strong physiological orientation and, equally important, they were among the first generation of German botanists to come of age, so to speak, within a Darwinian universe; they attended universities in the late 1870s and early 1880s, when Darwinism was enjoying its greatest popularity in Germany. With their backgrounds in plant anatomy and physiology, they saw in the concept of natural selection the key to explaining the manifold complex adaptations of plants to biotic and abiotic factors in their environments. Their Darwinism convinced them that every aspect of plant structure has a function in the living plant, and they set about developing programs to exploit the research potential of that principle. As much as any single group of biologists in the nineteenth century, this group of German botanists attempted to apply the concept of natural selection directly to their individual research projects. This was a relatively rare phenomenon, since the principal effect of Darwin's evolution theory had been to direct the attention of biologists to problems relating to *phylogeny*. In 1927, for example, British ecologist Charles Elton complained that Darwin's evolution theory had sent zoologists

flocking indoors for over fifty years (to search for phylogenetic relationships in comparative studies of external and internal animal structures) and that only recently had some of them begun to venture out into the open air to study animals in their natural surroundings.[5] The situation in botany was not nearly so bad, but it was certainly the case that few botanists had used the concept of natural selection as a justification for studying adaptation. Stahl, Haberlandt, Schimper, and their colleagues represent notable exceptions.

If Darwinism was an important stimulus for their ecological research, so also was their field experience in foreign lands. As a result of Germany's colonial expansion in the last two decades of the nineteenth century, opportunities developed for German scientists to carry on their research far beyond the political boundaries of the Reich. The botanists under consideration in this study were especially well prepared to take advantage of these opportunities, since they had a research program designed to investigate the relationship of environmental factors to organic form and function. Particular adaptations are often easier to recognize in organisms living under unusual or extreme environmental conditions; and most of the travel opportunities were in the tropics, where plants exist under conditions of heat and moisture quite unfamiliar to botanists trained in central Europe. Firsthand experience of the diverse array of adaptive phenomena exhibited by tropical plants, therefore, served to reinforce the environmental emphasis of their work. Their most important ecological studies involved non-European plants. Nevertheless, they continually stressed the need to apply the knowledge of plant adaptation gained in exotic lands to an understanding of adaptive phenomena in native European vegetation. They did not have practical applications in mind, at least not at first; they simply wanted to use their experience outside Europe to gain insights into the organization and behavior of the familiar plants upon which most of their anatomical and physiological knowledge was based.

This early Darwinian school of plant ecology was very much an outgrowth of the cultural and institutional settings in which it developed. Chapter 1 examines the major institutional and intellectual themes that served as the background for botanical work in Germany in the late nineteenth century. Important here was the professional development of botanical science during the third quarter of the nineteenth century and its relationship to the German university system. The researchers who turned their attention to studies of plant adaptation in the 1880s were all trained within a thorough laboratory tradition that had become the mark of German botany. This tradition was born of several causes – the reaction to speculative science, the improvement in microscopic technique, the development of research seminars and institutes within the German universities – and it was characterized by a cautious, inductive, compartmentalized approach to botanical problems. Once they received their training within this tradition, botanists could anticipate a lengthy period of internship before finding a permanent university appoint-

ment, since the number of professorships in botany, as in most fields, had not kept pace with the growing ranks of postdoctoral students. This long period without the security or the responsibilities of a permanent appointment may, in some cases, have encouraged research in nontraditional areas and contributed to extended botanical excursions in exotic regions.

In terms of influence and intellectual traditions, the German eco-physiological botanists fall into two broad groups. The first group consists of students of Simon Schwendener, who explored an approach to the study of plant life that they chose to call "physiological plant anatomy." This group was centered at Schwendener's botanical institute at the University of Berlin, although physiological plant anatomy itself was first developed by Gottlieb Haberlandt, who studied with Schwendener for a short period in Tübingen. Chapter 2 examines the careers of Schwendener and Haberlandt, their brief collaboration, and some of the difficulties that their research program encountered with proponents of the traditional compartmentalized approach to botanical research, which maintained the separation of anatomical and physiological investigations. Haberlandt, more so than Schwendener, was criticized for mixing together discussions of structure and function, a practice that he justified on the basis of Darwin's natural selection theory. Chapter 3 treats the Darwinian character of Haberlandt's work, and Chapter 4 surveys briefly the work and the personnel of the Schwendener school in Berlin. A number of Schwendener's students applied this new approach to botany outside the laboratory and outside the boundaries of Europe. Chapter 5 examines the research carried out by Georg Volkens in Africa and by Haberlandt in Java and Malaysia and briefly discusses the background of German colonial development.

The second group of plant adaptationists consists of students trained at Strasbourg and Bonn by Anton de Bary and Eduard Strasburger, neither of whom had a strong personal interest in the problem of adaptation. Two members of this group, A. F. W. Schimper and Heinrich Schenck, were longtime colleagues at Bonn who carried out extensive field research in South America. The third member, Ernst Stahl, had the good fortune to secure a permanent position relatively early at the University of Jena, where he conducted his research somewhat in isolation from the others. Chapter 6 follows Stahl's research from his early straightforward anatomical and physiological investigations under the direction of de Bary and Sachs to his elaborate studies of adaptive phenomena in Europe and abroad. Chapter 7 traces the careers of Schimper and Schenck, focusing on their research in the American tropics. These three together produced perhaps the most extensive and detailed Darwinian treatments of plant adaptation to be found among botanists in the late nineteenth century.

Chapters 8 and 9 concern the primary sources of motivation behind this ecological work: Darwinism and field experience in exotic lands. Chapter 8 examines particular examples of the use of the concept of natural selection to

interpret adaptive phenomena, the relationship between this approach to adaptation and that employed by German botanists earlier in the century, and the criticisms raised by contemporaries regarding this Darwinian school of plant biology. Those criticisms, for the most part, were directed at the teleological character of the plant adaptation studies, but the authors of these studies were convinced that Darwin's evolution theory justified the return to discussions of purpose in biological science. Chapter 9 considers the connection between these studies of plant adaptation and German colonial expansion. These botanists did not generally take an active interest in the economic development of the colonies during the period to which this study is confined. Instead, they took advantage of Germany's imperial venture to extend their research experience – to engage, as it were, in a kind of intellectual imperialism. However, their endeavors were aided considerably by scientific facilities, such as the Buitenzorg Botanical Garden, which were tied closely to the economic interests of the colonies.

In Chapter 10 I briefly point out some of the specific connections between the late-nineteenth-century German studies in plant adaptation and the early formal development of plant ecology, and I offer speculations regarding the broader relationship between these two movements. The central point here is that the appearance of a formal science of plant ecology in the early twentieth century can be viewed as the result of the integration, under favorable institutional settings, of the causal/functional approach to botanical science (as characterized by the work of these Germans) with the phytogeographical tradition of identifying and classifying natural plant communities. Although the United States served as the most active center of the new discipline, American plant ecologists, as well as those in England and Scandinavia, were influenced, directly or indirectly, by the ecophysiological studies that came out of Germany in the late nineteenth century.

Contemporary critics of neo-Darwinism, such as Stephen Gould, would characterize this group of German botanists as adaptationists; they strongly believed that their adherence to a strict selectionist view of organic transformation compelled them to regard virtually all plant structures as having adaptive significance.[6] As such, they differed from most of the early plant ecologists, whose positions regarding the mechanism of evolution varied between neutrality and Lamarckism. However, although the science of plant ecology may have drawn its formal lines during a period when Darwinism was out of favor, the practitioners of the new science were quite cognizant of the force of the Darwinian explanation for evolution and the attention it directed to the problem of adaptation. Although the focus of the new plant ecology was on the nature, rather than the origins, of adaptations, early plant ecologists made use of, and paid tribute to, the pioneering work of these late-nineteenth-century Germans, for whom Darwinism had been a primary factor in redirecting their intensive botanical training from the laboratory to the natural habitat

of the plant. Yet whatever their influence on twentieth-century ecological science, studies of the relationship between the living plant and its environment came about in Germany during the last two decades of the nineteenth century as the result of a combination of intellectual trends, professional concerns, and political developments peculiar to that time and place. This is as much a study of the history of German science, Darwinian biology in the late nineteenth century, the institutionalization of the life sciences in Germany, and the relationship between science and colonialism as it is a study of the early history of plant ecology. It is a profile of a group of similarly trained young scientists responding to a common set of intellectual influences and institutional pressures and taking advantage of particular political circumstances. The result of these influences and responses was the appearance, at the end of the nineteenth century, of a Darwinian school of botanical science that never found a permanent institutional home but that nevertheless influenced the development of plant biology and the new science of plant ecology well into the twentieth century.