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ANTHONY D-N

Ecology and the Professionalization of Botany in America, 1890–1905

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Part I: Introduction

During the 1890s, a growing number of American botanists turned their attention to a new area of study concerned with the adaptations of plants and the causal factors underlying local plant-distribution patterns. In 1893, a group of botanists meeting in Madison, Wisconsin, decided to adopt the word "ecology" to apply to this new field, a word that had been coined by Ernst Haeckel in 1866, but had been used very little in either Europe or America since then.[1] By 1899, the Nebraska botanist Charles E. Bessey, then botanical editor of *Science*, could write to his former student Conway MacMillan: "I am becoming dreadfully tired of the fad which has taken possession of many of our friends, leading them to suppose that ecology is *all there is* to botany."[2] While Bessey, a more traditional botanist, may have mistaken a growing genuine interest for a fad, any examination of the botanical literature published during the 1890s, especially that in the *American Naturalist, Botanical Gazette,* and *Science*, will reveal an increasing number of ecologically oriented papers, some of them of dubious quality. By 1903, one-third of the papers read during the botanical section at the meeting of the American Association for the Advancement of Science (AAAS) were devoted to ecological subjects, including such topics as "Ecological Notes on the Islands of Bermuda" and "An Ecologically Aberrant Begonia."[3] Perhaps by then ecology had, in fact, become a fad, at least among botanists. During this early period, the word "ecology" was often used interchangeably with "plant ecology" or "ecological plant geography." This is not to imply that

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other aspects of ecology received no attention at this time: it would be easy enough to cite isolated examples from limnology or studies of animal populations. Similarly, it would not be difficult to find examples of ecological literature before 1890.[4] However, ecology was first recognized and consciously pursued during the 1890s as a specialization within botany.

Historical accounts of the origins of plant ecology in America tend to concentrate on the work of two men, Frederic E. Clements and Henry Chandler Cowles, who, inspired by the example of certain late nineteenth-century European plant geographers, produced seminal studies of vegetation as graduate students at the Universities of Nebraska and Chicago, respectively, in the late 1890s.[5] The association of early plant ecology in America with Clements and Cowles is due largely to the extent of their influence on the subsequent development of the discipline and to their emphasis on what was to become the uniquely American aspect of plant ecology: the study of the dynamics of whole plant communities treated as functionally independent units. To a greater extent than their European counterparts, Clements and Cowles, and those who followed their lead, emphasized changes in community structure and composition over time and stressed the successional replacement of community types leading to the environmentally determined "climax." These concepts were to set the tone for ecological research among American botanists for the next forty years.[6]

While there is little question that dynamic plant ecology in America received its impetus from the work of Clements and Cowles, there is also little doubt that their work fell on a receptive audience. Clements and Cowles emerged as the central figures among a group of a dozen or so botanists who had begun to investigate ecological problems during the 1890s and early 1900s. Because this group was not well defined, and because subsequent work in plant ecology was dominated by the influence of Clements and Cowles, this early period has not received much attention in the literature, and the contributions of Clements's and Cowles's contemporaries have generally been ignored. The aim of the present study is to identify those American botanists who began to investigate ecological problems during the 1890–1905 period, briefly to examine their work, and to place that work within the context of the professional development of botany in the United States in the late nineteenth century. This study is restricted to the 1890–1905 period, a period during which the number of researchers was slowly growing, the subject matter of ecology was still somewhat ill-defined, and there were as yet no clearly acknowledged leaders. After 1905, the discipline became dominated to some extent by Cowles, through his teaching at the University of Chicago, and to a greater extent by Clements, through his theoretical writing, beginning with *Research Methods in Ecology*, in 1905.

One does not have to search far for hypotheses as to the origins of plant ecology in the late nineteenth century. To begin with, Darwin's discussion of the struggle for existence and the process of natural selection provided the justification and motivation for studying relationships among organisms and between organisms and environments. This was, after all, the reason for Haeckel's coining the word "ecology." Philosopher David Hull has pointed out that ecology is "the study of short-term evolution;" and at least one contemporary plant ecologist frequently exhorts his colleagues to turn to the *Origin of Species* for ideas and inspiration.[7] However, nineteenth-century botanists did not read the *Origin* and then dash out into the field searching for interrelationships. There was a sizable time lag, at least thirty years, between the publication of Darwin's book and the appearance of a significant body of ecological literature, and in those intervening years Darwin's ideas received a substantial amount of criticism. In fact, Michael Ghiselin has recently remarked: "Indeed, one can hardly even begin to understand modern ecology unless one realizes that this science developed much of its theoretical basis during the period from 1880 to 1940, when Darwin was out of fashion."[8] Yet despite Ghiselin's warning, if the connection between Darwinian evolutionary theory and the emergence of ecology is not a clear one, neither is the connection between ecology and some of the alternatives to Darwinism. Lamarckism, for example, was especially popular among American botanists in the late nineteenth century; yet a predisposition to Lamarckian explanations for species change does not appear as a driving force behind the ecological studies that emerge in the 1890s. Evolutionary theory, whatever the supposed mechanism for evolution, provided the broad background for all biological research in the late nineteenth century. Its influence on the emergence of a science of ecology by the end of the century was manifested indirectly by focusing the attention of biologists on the general problem of adaptation. While this was certainly an important influence, I believe that we must search elsewhere for the immediate causes for the emergence of plant ecology.

Another set of hypotheses arise from a consideration of the broader social and cultural contexts of late nineteenth-century America. The popularity of nature writing in the second half of the century, such as the work of John Muir and John Burroughs, reflected the interest of an increasingly urbanized and industrialized populace in the natural history of a continent that was gradually losing its wild places. This interest was manifested further in the creation of national parks and a system of national forests. By the 1890s, the conservation movement was gathering steam, and a movement for the preservation of wilderness areas and the protection of endangered species, led by John Muir and the newly formed Sierra Club, had also taken shape.[9] Certainly, botanists were aware of, and participated in, this general concern for America's natural environments. Yet, once again, the connection to the emergence of plant ecology is not clear. The published works of the botanists under consideration here do not reveal a strong sense of concern for the vanishing American wilderness.

Not seeking to discount Darwinism, Lamarckism, naturalism, and the

onservation and preservation movements as influences on the origin and development of plant ecology in America, I shall suggest an alternative hypothesis that has, to date, received very little attention. The growing interest in ecological problems among American botanists in the 1890s reflected a shift in American botany in general away from description and classification and toward studies of process and function. This shift had taken place earlier in Europe, especially Germany, and made its way to America in the 1880s. It manifested itself particularly in the development of plant physiology and plant pathology, but plant ecology also appeared as a logical offshoot of this emphasis on dynamic interactions. Field-oriented botanists, aware of the possible practical applications of ecology but, more importantly, also aware of the limitations of traditional botany and anxious to take part in the development of a viable plant science in America, found in ecology a natural outlet for their interests and abilities. To a large extent, then, plant ecology was a consequence of the maturation and professionalization of the science of botany in America. In what follows, I examine certain major trends in American botany during the last decades of the nineteenth century, providing thereby the essential context in which ecological work was pursued. I shall then introduce the discussion of the ecological work through an examination of the careers of those botanists who provided the intellectual leadership in this new field.[10]

Part II: The Professionalization of American Botany, 1870–1895

The American botanists who began to study plant ecology were for the most part younger members of a rising professional generation of botanists, a generation that had grown from an estimated half dozen full-time university professors in 1865 to several times that number by the 1890s, not to mention the numerous botanical specialists employed by the Department of Agriculture. Along with this growth in size came an increasing sense of community and mutual purpose. During the 1880s, botanists had begun to look upon themselves as a distinct professional group and had been meeting annually on an informal basis as the Botanical Club of the American Association for the Advancement of Science (AAAS). By 1892, that informal arrangement was formalized when the AAAS established a separate section (Section G) for botany. With a membership of approximately eighty-five, Section G met for the first time, with Charles Bessey presiding, at the AAAS national meeting in Madison, Wisconsin, in the summer of 1893.[11] The day after those sessions adjourned another meeting of botanists convened in Madison for the purpose of discussing botanical nomenclature. Originally called the International Botanical Congress, the name of the meeting was promptly changed to Madison Botanical Congress when it became evident that only two foreign botanists

were in attendance. In fact, only thirty-eight botanists in all attended this meeting, perhaps the result of competition with the World's Columbian Exposition in Chicago, to which many of those in attendance at the AAAS meeting quickly rushed as soon as that meeting had terminated. Whatever the reasons for the sparse attendance, one of the official actions of the Madison Botanical Congress was to adopt the word "ecology," with its anglicized spelling, to apply to "the general phenomena of plant development, the plant's relations to its environment, and its relations to other organisms."[12] This action came during a discussion of the terminology of plant physiology and acknowledged the need to separate this new area of study from the main body of plant physiological research. Thus, a handful of botanists, most of them from the Midwest, quietly introduced the term "ecology" into their language a few days after the professional community of American botanists held its first formal meeting.

Along with the growth of botany in terms of numbers of researchers and positions, there had been a considerable change in emphasis during the period preceding the emergence of plant ecology. The two fields from which the ideas of plant ecology were drawn—theoretical plant geography and plant physiology—had not long been associated with American botany. While in Europe phytogeography could be traced back to the work of men such as von Humboldt, Schouw, the elder de Candolle, and Grisebach, early in the nineteenth century, no such tradition existed in the United States. Certainly, many American botanists were aware of the work of these men, but phytogeography was not a central theme in American botany during most of the nineteenth century. Geographical work in botany emphasized floristic studies rather than discussions of the principles of distribution. Similarly, the plant physiology that had been developing in Germany since the 1860s, with Sachs, Strasburger, and others, did not make its appearance in America until the 1880s. Botanists in America had been preoccupied with the task of collecting and classifying the flora of the continent. Professionally trained botanists were in short supply, and the few botany professors in the United States in the mid-nineteenth century had all the work they could handle in cataloging the plants collected on the many government-sponsored expeditions into the western territories. As result, the teaching of botany emphasized those aspects of the subject necessary for systematic work, that is, the anatomy, morphology, and taxonomy of the seed plants.[13]

The first significant changes from the taxonomic tradition occurred in the 1870s and were initiated by students of Asa Gray, himself the most prominent representative of that older tradition. One of the most important of these changes was the introduction of laboratory instruction to the teaching of undergraduates. Charles E. Bessey (1845–1915) set up perhaps the first such botanical laboratory in the United States at the Iowa Agricultural College in 1871, only two years after the college had opened. Bessey, who later

studied with Gray at Harvard, received his initial botanical instruction at Michigan Agricultural College under William J. Beal, a former student of Gray. Beal, perhaps as the result of his contact with Gray and Louis Agassiz at Harvard, later authored a very influential pamphlet entitled "The New Botany," in which he encouraged experimental work and challenged the older methods of teaching, which often amounted to little more than rote memorization of passages from botanical texts. It is not clear how much of Bessey's outlook was derived from Beal, but he did set up his botanical laboratory after having studied with Beal and before meeting Gray and attending Harvard in the mid-1870s.[14]

Another of the changes characteristic of the "new botany" was the movement toward the study of the entire plant kingdom, not just the seed plants. Another of Gray's students, William G. Farlow (1844-1919), became the first professor of cryptogamic botany (the study of the algae, fungi, mosses, and primitive vascular plants) at Harvard in 1874, after returning from two years' study in Germany. The study of the cryptogams had recently come into vogue, because the publication of the *Origin of Species*, along with Wilhelm Hofmeister's work during the 1850s establishing the ubiquity of the alternation of generations among all forms of plant life, provided ample justification for the treatment of the entire plant kingdom as a single evolutionary unit. In addition, Louis Pasteur's work with microorganisms during the 1860s directed the attention of biologists toward the simpler forms of life. By 1886, a contributor to *Science* could report the following:

> Whereas only a few years ago botany, as a college study, dealt chiefly with the flowering plants and vascular cryptogams, its scope has broadened, even in the limited undergraduate curriculum, so that the graduate of today is supposed to have been taught more or less about each of the principal groups of plants, from the lowest to the highest, if he has studied botany at all. With this change has come an earnest effort to make his knowledge a working-knowledge, obtained in the laboratory so far as essentials are concerned, and merely rounded out in the lecture-room.[15]

Both of these aspects of the "new botany," that is, the study of the cryptogams and the introduction of laboratory instruction, were first introduced to American botanists at large in the form of a new textbook published by Charles Bessey in 1880. Bessey's *Botany for High Schools and Colleges* was based on an earlier text by German botanist Julius Sachs, perhaps the most influential botany text in the nineteenth century. Sachs's book gave equal weight to the cryptogams and phanerogams (seed plants), emphasized plant physiology, and employed a new classification scheme for the algae, fungi, and lichens.[16] William G. Farlow reported that on his return from Germany in 1874 the contents of Sachs's text was quite new in England and virtually unknown in America. An English translation of the text, which appeared in 1875, received a favorable review in the *American Naturalist*; but, perhaps

due to its high price, it never enjoyed a wide circulation in America. Instead, the ideas of Sachs's textbook made their way into American botany through Bessey's text, which has been characterized as "the most successful textbook of botany published in the United States between 1880 and 1910."[18] The text was an immediate success and was reprinted in seven editions over the next twenty-five years. When it first appeared, the editor of the *Botanical Gazette* stated: "We would most cordially recommend the work to the use of all professors and students of botany as not only the *best* American book upon the subject, but the *only* one." Asa Gray, to whom the task of writing an American adaptation of Sachs had first been suggested, stated in a review: "The work concerns itself throughout with what the Germans call 'Scientific Botany,'—largely with vegetable anatomy and development, and with particular attention to the lower Cryptogamia"; and he added that the classification scheme employed by Bessey represented an improvement over Sachs. The review in the *American Naturalist* stated: "It is well adapted to give one who has but little special knowledge of botany a clear conception of the plant as an organism."[19]

This last remark is worth noting. The concept of the organism is central to biology and reflects the difference between the older natural history tradition and the "scientific" study of living things. During the 1870s and 1880s, biology was superseding botany and zoology in importance in Great Britain and America, largely through the example set by Huxley, Lankester, and Martin in England, and such American proponents as W. K. Brooks at Johns Hopkins. W. G. Farlow spoke of a "biological epidemic" which occurred shortly after his return to America in the 1870s and threatened many botanical appointments. Apparently, university administrators, identifying "biology" with a superior breed of scientist, were finding it economically expedient to call their zoologists "biologists" and eliminate botanical positions altogether. Conway MacMillan, a student of Bessey and professor of botany at the University of Minnesota, was still complaining about this situation in 1893, when his article in *Science,* concerning this "sham biology," as he called it, inspired a heated exchange of letters.[20] The conceptual attraction of biology was that it was closely associated with physiology, and physiology, in turn, with physics and chemistry. Yet whatever the fate of particular university chairs in botany, Bessey's textbook went far toward establishing plant biology in America. By stressing observation and experiment, by stressing physiology, and by discussing the entire evolutionary spectrum of the plant kingdom, it had the effect of lending to the subject of botany greater scientific authority.

Bessey's own interests still centered on taxonomy or, more correctly, classification. As Asa Gray had indicated in his review, one of the achievements of Bessey's text was to rework some parts of the classification system used by Sachs. In an address to the botanical section of the AAAS in 1893, Bessey

stated: "The work of the morphologist and the physiologist no less than that of the professed systematist all find their expression in classification." He was interested in determining the correct phylogenetic arrangement of the flowering plants and published one of his best statements on the subject in 1915, the year he died.[21] Nevertheless, his appointments at Iowa Agricultural College and the University of Nebraska, two land-grant institutions, put him in a position to consider more practical problems as well. At Nebraska Bessey and his students participated in a botanical survey of the state, which had been conceived as a service to the agricultural community. Surveys of vegetation for the purpose of determining the suitability of land for various types of agriculture, as well as for assessing and controlling the spread of weeds, were becoming an important part of the task of university botany departments and experiment stations in the Midwest. Similarly, the study of the cryptogams was of considerable aid to the farmer in contributing to the understanding and control of the diseases of crop plants. Bessey and other botanists in his generation were constantly in touch with these practical problems and were directing their students toward the new areas of study that they created.[22]

Much of the practical work was carried on at the new agricultural experiment stations created by the Hatch Act of 1887. While work at the stations necessarily varied from state to state, there were important similarities, as this excerpt from an 1891 report attests: "In the first place, the Association of the American Agricultural colleges and Experiment Stations held a four days' convention, and during the opening session there was a report of the chairman of the botanical section of the work done at the various stations by the botanists thus employed. It was evident from this report that while systematic botany, making of collections, and the field study of various plants were important features, the main one in several states is the study of the fungus enemies of cultivated crops."[23] Early breakthroughs in the study of plant diseases at the experiment stations had made Americans leaders in this field. In his vice-presidential address to Section G of the AAAS in 1895, plant pathologist J. C. Arthur indicated that the stations were promoting other studies as well, stating: "American botany owes much to the Agricultural Experiment Stations, especially in promoting a knowledge of vegetable pathology and ecology."[24] Unfortunately, Arthur did not elaborate upon what the stations were doing with regard to ecology. Judging from the context of his address, he probably had in mind studies of the effects of such factors as soil chemistry, moisture, and light on the growth of crop plants. In any case, the study of ecology may have received an important stimulus from the practical concerns of agriculture.

There were other, equally important, concerns, however, which contributed to the shift in botany from its older emphasis on taxonomy. W. G. Farlow made a plea for the study of plant physiology on the basis of its possible contribution to the professional advancement of botanical science in America. He stressed the need to catch up with European botany and pointed out that there were not a half-dozen botanical laboratories in America adequately equipped for physiological research. That was in 1887. Vegetable physiology, as the subject was called in the nineteenth century, had been discussed in Bessey's 1880 textbook, but it had not yet become a major field of interest. The subject was in fact introduced in the United States in 1873, when George L. Goodale initiated a course in vegetable physiology at Harvard. Goodale (1839–1923), a student of Asa Gray and later the successor to his chair at Harvard, also wrote a plant physiology text in 1885, perhaps the first such text published in the United States. Yet in 1887 Farlow was concerned that the subject had not yet attracted the attention of many younger botanists, and he offered an explanation: ". . . when we consider that, as a nation, we are noted for our inventive powers and fondness for studies having a practical bearing, it seems a little strange that vegetable physiology has not had a larger number of followers with us. Possibly the attractions of physics and chemistry have drawn away some who might have done good work in physiology."[25] Although he mentioned the practical side of plant physiology, Farlow emphasized the importance of the advancement of American botany, stating that the most urgent need in America is "to raise the standard of work in this country to that of countries in which botany has reached its highest development."[26]

The "highest development" was, for Farlow and many others, physiology. Physiology represented the closest association between the biological and the physical sciences. In an attempt to characterize the nature of the advances made in general physiology in the mid-nineteenth century, British biologist J. S. Burdon-Sanderson echoed the sentiments of many of his colleagues when he remarked, in an address in 1893, "that progress was rendered possible by the rapid advances which, during the previous decade, had been made in physics and chemistry, and the participation of physiology in the general awakening of the scientific spirit which these discoveries produced."[27] It was physiology that separated the biological sciences from natural history. The study of process and function, the use of the laboratory, the experimental method—these were held to be the ingredients of true science. Plant physiology had obvious practical applications, such as the determination of the exact nutritional requirements of crop plants, but its association with the physical sciences held equal, or even greater, attraction. J. C. Arthur, in the 1895 address cited earlier, stated: "The present great advance in the science may, in large measure, be traced to the wonderful advances in the sciences of chemistry and physics, which have supplied facts and methods to assist the physiologist in his study of life processes"; and, he added, that although physiology is not dependent on chemistry and physics, nevertheless, "the path of present advancement keeps steadily onward in the clear light of physical laws, and ignores the nearness of mystical, unfathomable shadows."[28]

Despite Arthur's flare for the melodramatic, his words reflected a general feeling among American botanists that the development of plant physiology represented the final stage in the maturation of botany as a science. One of the purposes of Arthur's address was to demonstrate why plant physiology deserved to be included in a liberal education, along with the other natural sciences. He was not happy with the progress made thus far, stating quite bluntly, "So far as America is concerned there is no research side; the science is equipped with facts and theories from foreign sources";[29] but he added that some research work had been done by graduate students in recent years. The situation was improving from the point of view of formal organization. In 1895, the *American Naturalist* added an editor in vegetable physiology to its staff and included, for the first time, a section under that heading in its short reports of recent work. Two years later the recently organized Society for Plant Morphology and Physiology held its first meeting in Philadelphia and elected William G. Farlow its first president.[30]

Most of the organizational work for that meeting had been done by William F. Ganong, a former student of George Goodale, who contributed some important papers to the ecological literature around the turn of the century. It is not surprising that Ganong, primarily a plant physiologist by training, should show considerable interest in ecology. Ecology at this time was closely associated with physiology and represented, at least in the minds of botanists, a kind of field-centered extension of this laboratory-centered science. As I have mentioned earlier, the word "ecology" was first adopted by American botanists during a discussion of the terminology of plant physiology. The committee that initiated that action at the Madison Botanical Congress was comprised of J. C. Arthur, a professor of vegetable physiology and pathology at Purdue; Charles R. Barnes, a plant physiologist at the University of Wisconsin; A. S. Hitchcock, a botanist at the University of Kansas, who later became a specialist in grasses for the United States Department of Agriculture (USDA); Conway MacMillan, a botany professor at the University of Minnesota, who had recently written an ecologically oriented study of the vegetation of Minnesota; and W. T. Swingle, a plant pathologist with the USDA. The composition of this committee reflects the extent to which the study of botany had diverged from taxonomy by the 1890s. Some of the discussion that took place concerning ecology merits repeating. Hitchcock introduced the problem as follows:

There is a certain part of physiology which deals with the chemical and physical problems of the plant and not with the more strictly vital problems. . . . This the committee would call physiology proper. The remainder of the subject as usually treated has been called plant biology by the Germans. The subject matter is familiar enough, but it is rather difficult to give a definition showing its limitations. It concerns itself with the adaptive processes of the plant, and with what the Darwinian school has brought forward and made popular. What we want is a term for this latter part of the science.[31]

Charles Bessey, who was sitting in on the discussion, asked for a cl statement of the distinction between these two aspects of physiology. A some further discussion MacMillan added:

In my mind the difference between these two divisions of physiology is one which must constantly shift with a wider knowledge of physiology. It is a very convenient distinction for our present purpose. We speak of physiology as embracing the chemical and physical relations of the plant, i.e., it is the chemics and physics of plant life. It is recognized that there is a group of phenomena very essentially different from the group which we place under the general head of physiology. These have to deal with the interrelations of organisms and their mutual adaptations. To separate these two groups it is desirable to use the term ecology. It is primarily to supplant the use of the term biology in its restricted and less proper sense that this other term is brought into use.[32]

Thus, in a sense, ecology represented the application of the science of physiology to the broader question of adaptation.

As the above quotations indicate, German botanists had been using the term "biology" to apply to this field of study; and the members of the committee considered this a misuse of the term. Other terms had been suggested to remedy this problem. The Scots botanist Patrick Geddes, acting on a suggestion from Ray Lankester, favored the term "bionomics," and one finds occasional references to bionomics in the literature into the early twentieth century. William F. Ganong, an American botanist who had not been present at the meeting in Madison, suggested "phytobiology," but that term gained almost no supporters.[33] More significant than the problem of terminology, however, is the fact that these botanists were concerned that there was a new field of inquiry, closely aligned with physiology, that was in need of definition and exploitation. The ecologist was to be a kind of outdoor physiologist who made measurements, recorded the responses of plants, and tried to show functional relationships between the structure and responses of individual plants, or groups of plants, and various environmental factors.

Part III: Ecology in American Botany, 1890–1905

Despite the expectations of the Committee on the Terminology of Physiology of the Madison Botanical Congress, the actual ecological work done by botanists during the 1890s and early 1900s was uneven in quality, often descriptive, and much less sophisticated than laboratory physiology. This work ranged from studies in ecological plant geography, which attempted to relate broad patterns in the plant cover of a region to various environmental factors, to more restricted studies in physiological ecology, which attempted to monitor the effects of particular environmental conditions on individual plants or small groups of plants. There were fewer studies that fell clearly into the latter category, and most of the work fell somewhere in between. In

is of influence and tradition, most of the ecological work was done by tanists in one of three somewhat loosely united groups. The first of these includes a few Washington-based botanists who were associated with the Department of Agriculture, and later with the Carnegie Institution as well. The second group includes students of Charles E. Bessey, three of whom made significant contributions to the ecological literature during this period. The third group includes botanists whose interest in ecology was stimulated primarily by the very popular plant ecology text published by the Dane Eugen Warming in the late 1890s. Some of the botanists who did ecological work during this period fit into more than one of these groups and a few others defy classification. In what follows, I shall offer a brief characterization of the careers of the young botanists who were entering ecology and then examine general themes common to their endeavor. Ecology, I should add, was but one of several specializations open to the professional botanist during the late nineteenth century. Although there was a marked increase in ecological research during the 1890s, many botanists were finding careers for themselves as specialists in plant pathology, in plant physiology, in mycology and phycology, and in experimental plant breeding, not to mention such traditional areas as morphology and taxonomy; and many of these botanists showed little interest in the ecological point of view.

Ecology and the USDA

In 1890, a planned expedition into the Death Valley region, to be conducted by the Division of Ornithology and Mammology of the Department of Agriculture, added to its staff the young botanist Frederick V. Coville. Coville (1867-1937) had been with the USDA since 1888, shortly after graduating from Cornell.[34] The expedition was carried out in 1891 under the leadership of C. Hart Merriam, the director of the Division of Ornithology and Mammalogy, and two years later Coville published a lengthy report of his findings in *Contributions from the U.S. National Herbarium*. Coville's report reveals the influence of Merriam, who in recent years had been making speculations concerning the division of the North American continent into specific life zones. Coville accordingly attempted to relate his findings concerning desert flora to the system of faunal zonation that Merriam had devised. Merriam was convinced that temperature was the major limiting factor and had organized the Death Valley trip, in part at least, in order to test this hypothesis.[35] Coville's report, however, gave equal weight to such factors as soil, moisture, and light in determining the limits of distribution and discussed the specific structural and behavioral adaptations of desert plants to their arid habitat. He was particularly interested in the problem of spacing:

> The scantiness of the desert vegetation possesses more significance than has ever been attributed to it. Except in rare instances the shrub is separated from its nearest neighbor by a distance of several meters. Never do they stand so close together as to crowd or shade each other. . . . It is evident therefore that desert shrubs essentially present in their environment that anomaly of a struggle for existence, not against other plants, but against nonorganic physical forces alone. This fact makes the study of their adaptations especially interesting and instructive, for one element in the usual complexity of environment is removed, and we are able to perceive the simple influence of climate and soil conditions.[36]

Thus Coville was not only interested in other factors besides temperature, he also wished to relate the physiognomy and local distribution patterns of desert flora to the broad problem of adaptation.

After completing his report, Coville stayed on in Washington, taking the place of the late George Vasey as curator of the National Herbarium, an institution affiliated with the Department of Agriculture. Coville did not follow up his Death Valley study with additional studies of the adaptations of desert plants, but was preoccupied with his duties at the Herbarium. In 1898, he hired an assistant, Thomas H. Kearney, who also came under the influence of C. H. Merriam. Kearney (1874-1956) had been with the USDA since 1894 as an assistant agrostologist (specialist in grasses). Before that he had spent some time collecting in the Kentucky mountains and assisting N. L. Britton in the herbarium at Columbia University. In 1899, he accompanied Coville on a scientific expedition to Alaska, which was organized and led by Merriam. Kearney was to spend most of his career as a physiologist with the Bureau of Plant Industry of the USDA, but while working under Coville, he carried out ecological investigations into some of the more remote regions of the Southeast. Two significant papers emerged from these investigations, one dealing with an expedition to Ocracoke Island off the coast of North Carolina and the other with an expedition to the Dismal Swamp region in North Carolina and Virginia. Kearney's papers make frequent references to Merriam's theory of life zones, but, like Coville, he went beyond a one-factor analysis and discussed the various anatomical and physiological adaptations of plants to coastal and swamp conditions, citing the work of a number of European botanists in this regard.[37]

In 1903, Coville returned to the Southwest to help set up the Desert Botanical Laboratory of the Carnegie Institution near Tucson, Arizona. He had had the idea for such a laboratory since the Death Valley Expedition in 1891, and when the Carnegie Institution was established in Washington in 1902, he immediately presented it with a plan. His collaborator on the project was Daniel T. MacDougal (1865-1958), a plant physiologist who had studied with J. C. Arthur at Purdue. MacDougal's acquaintance with desert plants began in the summers of 1891 and 1892, when he explored the Arizona and Idaho regions for the USDA. He then went to the University of Minnesota as an instructor in botany under Conway MacMillan. After completing his Ph.D. degree at Purdue in 1897, he made two trips to Europe to inspect

botanical laboratories and modes of instruction in plant physiology. He returned to the West in 1898 to study the desert and alpine flora of Arizona, making measurements of the transpiration rates of plants and recording temperatures of the soil, air, and plant bodies. He then worked for a brief period with the New York Botanical Garden and, finally, became associated with the Carnegie Institution—first to set up the Desert Botanical Laboratory with Coville and then to direct the Laboratory in Plant Physiology, a position which he held for twenty-three years. While MacDougal was the author of several texts and numerous papers on plant physiology, his ecological writings include a study of the effects of light and darkness on plants (praised by Henry C. Cowles as one of the most important contributions to plant ecology during 1903) and a study of the distribution patterns and adaptations of desert plants, based upon work carried on at the Desert Laboratory.[38] The opening sentence of that last work explained the need for an outdoor research laboratory: "Botanical science in its technical and applied branches has reached a stage of development in which it has become plainly evident that adequate progress in research in physiology, in comprehension of life-histories, and in formulating the general principles governing the origin, environic relations and distributional movements of plants may be expected only by experimental methods in the field or in actual contact with the types of plants under consideration under normal environmental conditions."[39] MacDougal went on to say that whereas the study of plants in laboratories and greenhouses has made considerable progress, nevertheless there are certain questions, such as those outlined in the above quotation, whose answers require extensive investigations in the field.

Students of Charles E. Bessey

Although Charles Bessey's own research interests remained within traditional areas of botany, he encouraged a number of his students to pursue some of the newer fields, such as physiology, plant pathology, and ecology. Conway MacMillan (1867–1929) was the first whose work took a strong ecological orientation. MacMillan studied with Bessey at the University of Nebraska in the two years 1884–86, immediately after Bessey arrived at Nebraska from Iowa Agricultural College. MacMillan received the first master's degree ever awarded by the University of Nebraska in 1886.[40] Although the subject of his thesis was butterflies, he developed a deep interest in botany as a result of his association with Bessey. He went on to Johns Hopkins and Harvard for additional graduate study and in 1887 was hired as assistant professor in botany at the University of Minnesota. From 1891, at the age of twenty-four, until his resignation in 1906, MacMillan was head of the Department of Botany and the State Botanist of Minnesota. During that

time he maintained a regular correspondence with Bessey, who encou[illegible] him at every turn. In 1906, however, disappointed by the small finan[illegible] rewards of academic life and by his failure to communicate with sho[illegible] sighted administrators, MacMillan resigned his post at Minnesota to join an advertising firm in Philadelphia.[41]

MacMillan's ecological work began with a survey of the vegetation of Minnesota, which he published as *The Metaspermae of the Minnesota Valley,* in 1892. Bessey gave the book a favorable review in the *American Naturalist,* and throughout the next decade American and European botanists frequently cited it as one of the first examples of a regional survey of vegetation that went beyond a mere listing of species. To begin with, as the title implies, MacMillan chose as the limits of his region of study not the political boundaries of the state of Minnesota, but the drainage basin of the Minnesota River. In addition, he included a section on "the dynamic inter-relations of plants," in which he discussed a broad range of biotic and abiotic factors that help explain the repopulation of the area after glaciation. He then gave an account of plant competition on a hemispheric scale, describing tension zones at the interface of large-scale lateral and north-south migration patterns of whole systems of vegetation. The next year he published a paper in the *American Naturalist* that further discussed "tension zones" or "tension lines" between major plant formations and provided an explanation for the distribution patterns of plants during the Cretaceous period. Recognizing the importance of this paper, Bessey, as botanical editor of *American Naturalist,* pushed it into print ahead of others that had been waiting on his desk.[42]

MacMillan's main ecological interest was in the problem of zonation, not large-scale zonation such as Merriam's life zones, but localized zonal patterns such as those around a swamp or a pond. His most complete work on that subject was a lengthy study of the patterns of plant distribution along the shore of the Lake of the Woods at the border between Minnesota and Ontario. This work was later acclaimed by German phytogeographer Oscar Drude as the first significant ecological study in America.[43] MacMillan said as much in the conclusion of his paper: "Such an account, the first of its kind published in America, may be of service in stimulating ecologic study of plants, and if it be so fortunate its author will be well satisfied and repaid for some months of arduous work in the field. There is no question that the study of plant distribution over limited areas must be pursued more laboriously than ever, if the large problems of distribution are to receive accurate and authentic solution."[44] MacMillan did not produce any additional studies of local plant distribution patterns, but he did publish a more popular treatment of the vegetation of Minnesota. *Minnesota Plant Life,* which appeared in 1899, covered many of the same topics as *The Metaspermae of the Minnesota Valley,* but the style was much less formal, since the book was intended for a large nonprofessional audience.[45] The ecological orientation remained,

however. The book opened with a chapter entitled "Plants in their Societies," which dealt with the general laws of plant distribution and then discussed tension zones created at the interface between forest and prairie communities. MacMillan later confided in a letter to Frederic Clements, the eventual successor to his position at Minnesota, that he abandoned the approach of *Metaspermae of the Minnesota Valley* for that of *Minnesota Plant Life* because the administrators at the University of Minnesota were not terribly fond of erudition.[46]

Whatever the reasons for the change of style, the book was well received. It was Clements, in fact, another of Bessey's students, who reviewed it for the *American Naturalist.* Frederic E. Clements (1874-1945) had become something of an authority on ecological plant geography as a result of his publication, with Roscoe Pound, of *The Phytogeography of Nebraska,* in 1898. At the University of Nebraska, he and Pound had been members of an informal group called the Botanical Seminar, begun by Bessey and his students in 1886. Among other activities the Seminar conducted the Botanical Survey of Nebraska as a service of the state's agricultural community. Roscoe Pound (1870-1964) was head of the Survey, which collected the information about the state's vegetation that he and Clements compiled in *The Phytogeography of Nebraska.* That book served as a joint doctoral thesis for the two men. Pound went on to a prestigious career in law as dean of the Harvard Law School. Clements taught at Nebraska for a while, then became head of the botany department at Minnesota, after MacMillan left. In 1917, he joined the Carnegie Institution, where he remained until his retirement in 1941.[47]

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The Influence of Warming

Hitchcock's ecological study was one of several studies of regional vegetation that appeared in America in the years following the publication of Warming's text. As the original Danish title, *Plantesamfund* (plant communities or societies), implies, Warming's text emphasized the interrelationships of plants living in close association with one another. The plant community was a vital interconnected unit not a loose aggregation. For reasons that are not clear, the 1896 German edition used as its main title the subtitle of the Danish edition and was called *Lehrbuch der Oekologischen Pflanzengeographie.* When the English translation appeared in 1909, it was given the title *Oecology of Plants,* perhaps reflecting the preeminence that the term "ecology" had achieved by that time.[50] In any event, it was the German edition, not the English edition, that had the most influence on American botanists.

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This physiographic plant ecology emphasized successional change. Cowles's study of the plant communities along the continually shifting sand dunes of Lake Michigan had given him an excellent opportunity to examine such change, but he wished to extend this model to other areas as well. After all, even while examining apparently stable regions of vegetation we can speculate as to the developmental process by which the present plant communities became established. As Cowles stated this concept: "There must be, then, an order of succession of plant societies, just as there is an order of succession of topographic forms in the changing landscape. As the years pass by, one plant society must necessarily be supplanted by another, though the one passes into the other by imperceptible gradations."[52] This point of view is clear in the work of two of his students, H. N. Whitford (1872-1941) and Edgar N. Transeau (1875-1960). In 1901, Whitford published the results of a study of the development of forests in a region of northern Michigan that he had undertaken specifically to test some of Cowles's hypotheses regarding forest succession. Transeau chose to study larger patterns of vegetation, but his papers on the distribution of bog societies and on the centers of forest distribution, published in 1903 and 1905, respectively, reveal the influence of both Cowles and Warming.[53] Whitford, after completing his graduate work at Chicago in 1903, went on to a career with the Bureau of Forestry where his research took on a physiological orientation. Transeau was associated with Cowles for only a short time at Chicago and then went on to the University of Michigan to complete his graduate work. He spent most of his academic career teaching plant ecology at Ohio State University.

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Other Ecological Work in American Botany

Some of the ecological work carried on during the 1890-1905 period does not fit clearly into any of the above traditions. For example, in the early 1900s Volney M. Spalding, a plant physiologist at the University of Michigan, encouraged two of his students to undertake an ecological investigation of some small lakes in Michigan. Although not himself an ecologist, Spalding later became engaged in physiological research on the adaptations of desert plants at the Desert Laboratory of the Carnegie Institution. He had received his Ph.D. at Leipzig in 1894; however, his interest in ecology was derived not from European sources but from reading MacMillan's Lake of the Woods paper in 1897. He then encouraged L. H. Weld and Howard S. Reed to examine the vegetation surrounding certain lakes in southern Michigan. Weld did not remain at the university long enough to complete his part of the study and published only a preliminary report. However, Reed (1876-1950) prepared a more theoretical report that reveals not only the influence of MacMillan, with regard to the problem of the zonation of vegetation around a lake, but also that of Cowles and Warming, with regard to the concepts of plant societies and plant succession. In 1905, Reed published a short history of plant ecology that is notable in that it gives very little credit to the work that was being done in America. Similarly, Spalding, as the outgoing president of the Society for Plant Morphology and Physiology, in 1902, gave a talk entitled "The Rise and Progress of Ecology," in which he mentioned only MacMillan by name among the American contributors and concentrated on the work of Europeans. Apparently, it was still too early to tell whether ecology would be more than a passing fad in America.[55]

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After receiving a bachelor's and master's degree from the University of New Brunswick, both in zoology, he went on to Harvard, where he switched to botany. From 1887 to 1893, he was an assistant and then an instructor in botany under George L. Goodale. He then studied for a year in Germany, receiving his Ph.D. at Munich under Karl Goebel, in 1894. His interest in ecology was clearly the result of his exposure to German plant biology. His doctoral dissertation dealt with the special adaptations of cacti to the extremes of heat and aridity, a problem that Goebel had introduced in an earlier publication.[56] In a modified version of his dissertation, which Ganong published in the *Botanical Gazette* the following year, he outlined the additional research that is necessary:

> There is needed first and most important of all, an exact investigation into the meteorological and biological conditions under which the Cactaceae live. An all the year round study of the amount and time of rainfall, dew-formation, dryness of the air, winds, extremes and means of day and night and seasonal temperatures, intensity and amount of light, the kinds and habits of enemies and cross-pollinating and disseminating friends, the exact situations in which they grow and the nature of the soil, all these must be known about any district before we can more than guess at the "adaptations" in the Cactaceae which inhabit it.[57]

Ganong chose to call such studies of the interrelationships between plants and their environment "phytobiology" before the term "plant ecology" came into wide use. While still in Germany he initiated a series of articles for a Canadian journal on the subject of phytobiology, encouraging amateur botanists to undertake local ecological investigations, since taxonomy had become too complicated.[58]

On returning to America, Ganong took the position at Smith College, for which Goodale had recommended him, and then proceeded to establish an instructional program in botany there, to direct the botanical garden, and to manage the greenhouse, adjacent to which he set up a small botanical laboratory. His own research interests drifted more and more toward physiology—he taught the plant physiology courses at Smith and patented several pieces of laboratory equipment; nonetheless, he indicated his continued interest in ecology by entitling a 1901 physiology text *A Laboratory Course in Plant Physiology, Especially As a Basis for Ecology.*[59] During the summers, he made long excursions into the New Brunswick woods, taking copious notes and then publishing many of them in revised form in the *Bulletin of the Natural History Society of New Brunswick.*[60] These "Notes on the Natural History and Physiography of New Brunswick," 138 of them in all, covering a period of twenty years, contain an interesting mixture of ecological insight, natural history, and folklore. Ganong published several short papers on ecological subjects, and he did take the time to make one full-scale ecological in-

vestigation. This was his study of the vegetation of the salt marshes of [the Bay] of Fundy. Henry C. Cowles considered this one of the most important co[ntri]butions to plant ecology in America and stated: "The completeness of de[tail] and the accuracy of statement in Ganong's paper may well serve as models [to] working ecologists." Ganong conducted the field work for this study in the summers of 1899, 1900, and 1901 and then took two additional years to publish his results. The paper included a careful study of the physiological responses of marsh plants to various physical factors and made a plea for further study that might lead to a quantitative assessment of biological factors, that is, competition and cooperation.[61] Ganong himself undertook no further ecological investigations, however. Aside from a few short theoretical articles his ecological publications end with the Bay of Fundy paper.

* * * * *

The preceding was not intended to be an exhaustive discussion of early plant ecology in America, but I believe that I have included all of the botanists who made significant contributions to the ecological literature during the 1890–1905 period. It should be clear that most of these individuals had other interests in botany beside ecology. Some of them, such as MacMillan and Ganong, worked their ecological research around heavy teaching schedules and administrative responsibilities. Others, such as Kearney, Reed, and Whitford, pursued ecology seriously for a while and then went on to other areas of botany. Only Cowles, Clements, and Transeau were ever employed as plant ecologists. Also, these were western botanists for the most part. All but Ganong, Harshberger, and Kearney were either involved in research or connected with universities in the midwest or west. Of the thirteen men considered in this study, nine of them received their graduate training in midwestern universities, and six of the nine went on to hold university appointments in the midwest. In addition, these were young men. Their average age in the year 1900 was thirty, Ganong being the oldest at thirty-six, Reed, the youngest at twenty-four. These generalizations are not surprising. The botanists who became involved in ecological research during the 1890s and early 1900s were the students of botanists such as Bessey, Coulter, and Goodale, whose generation initiated the break from the traditional emphasis on taxonomy and morphology. Like their teachers, most of them found employment in the newer state universities that were either opening up or expanding in the midwest. While the work they produced was, on the whole, not extremely sophisticated, and while many of them went on to other fields, their interest in ecology during the period of this study is an indication that, at the end of the nineteenth century, botany in America had matured as a science to the extent that it could attempt to apply the techniques of physiology to the complex problem of adaptation.

Part IV: Ecology Defined

If a consistent ecological methodology had not yet emerged during this early period, and if most of the work fell far short of the ideal of a mature science, there was, nevertheless, considerable agreement among botanists as to the nature and purpose of ecology. It should be clear, first of all, that most botanists considered ecology a special branch of physiology that arose as the result of attempts to understand the functional relationships between plants and the physical and biotic conditions of their habitats. British botanist J. Reynolds Green summed this up nicely in his continuation of Sachs's *History of Botany:*

> Later in the century arose a development of physiology which now bids fair to assume a high degree of importance. The study of the individual plant gave way to some extent to the investigation of the mutual relations of plants growing together in some kind of association, and to the study of the vegetation of some particular environment as a whole. This was a departure at once novel and fascinating. It attracted the attention of many of the younger school of botanists and was pursued with much diligence under the name of *Oecology*. Many of the more obscure problems of physiology needed approaching from this standpoint.[62]

We do not generally make this association between ecology and physiology today, yet it was an important part of the vocabulary of early plant ecology. In their study of the Nebraska vegetation, Pound and Clements included the following explanation: "Ecology can not be set off sharply from physiology. Indeed, it is simply that particular phase of physiology which is manifested in the structure and habits of plants in their various homes. It is preeminently the division of phytogeography which seeks the connection between causes and effects."[63] Elsewhere Clements stated flatly: "There can be little question in regard to the essential identity of physiology and ecology." In a 1908 article, Cowles offered the same opinion, stating: "It is coming to be realized that the problems of physiology and ecology are identical."[64] We have perhaps become accustomed to associating physiology with researchers in white laboratory coats concentrating a battery of complicated equipment on the study of some minute subcellular process, but these turn-of-the-century botanists had in mind the functional responses of the whole plant to its external conditions. It was a logical next step to extend this point of view to the plant, or plant community, in its natural setting.

This broader view of physiology, as the above quotation from Pound and Clements indicates, necessarily leads one into a discussion of causes and effects. If we seek to explain, rather than merely describe, patterns of vegetation, then we get into the larger and more complex problem of adaptation. Accordingly, Hitchcock, during the 1893 Madison meeting, said of ecology: "It concerns itself with the adaptive processes of the plant, and with what the

Darwinian school has brought forward and made popular." Cowles later stated: "If ecology has a place at all in modern biology, certainly one of its great tasks is to unravel the mysteries of adaptation. Are the many structures of animals and plants, which are obviously of use, fundamental or accidental in an evolutionary sense?"[65] Although most of the ecological studies produced during this early period went little further than to describe particular adaptations or to state that certain types of vegetation are usually found in certain types of environments, the ideal was to explain why this is the case, both from a functional and from a phylogenetic standpoint. While most of the early plant ecologists gave some indication that the explanation of adaptation should be the ultimate goal of their science, Ganong was the most insistent. In 1903, he devoted his presidential address to the Society for Plant Morphology and Physiology, entitled "The Cardinal Principles of Ecology," to a discussion of the problem of adaptation. He expressed disappointment that ecology had not yet fulfilled its aim: "I believe it is a fact that, despite our numerous ecological publications, the only material advances made in ecology in this country for some years past are in descriptions of vegetation, in which a considerable body of fact has been accumulated. But in interpretation, the very soul of ecology, we have done little else than continue to kaleidoscope the old and familiar matter. Yet the aim of ecology is perfectly definite, and as lofty as any in science, being nothing less than to explain why each plant is what it is, where it is and in the company it is."[66] He believed that the proper approach to the solution of this problem was to carry out precise investigations of environmental conditions, to compile physiological life histories of particular plants, and to develop a method for correlating the two; and he praised the Carnegie Desert Laboratory as the kind of institution necessary to carry out this program.

Although this ideal of an ecological science that could explain the physiognomy, distribution, and abundance of particular species and plant societies was still far from realization, a number of botanists during this period were convinced that ecology would someday prove to be of great practical value. In his first paper on phytobiology, in 1894, Ganong, writing from Munich, stated: "Through the studies of the younger professional botanists, particulary of Europe, there is being developed the new department, almost the new science, of Phytobiology. It offers in the highest degree opportunities of great usefulness, and it is to be moreover the leaven of the botany of the future."[67] During the discussion of ecology at the 1893 meeting in Madison, J. C. Arthur said of ecology: "It is the phase of physiological botany in which we are especially interested as practical workers."[68] He elaborated upon this theme further in his 1895 address at the AAAS annual meeting: "What has been done for pathology [by the agricultural experiment stations] is likely to be done for ecology, as it is the second subject in importance cultivated by station botanists. In the latter science the assistance of the Agricultural Col-

leges is also important, for in a few years the subject will undoubtedly hold a commanding position in the curriculum of the agricultural and general science courses of these institutions, and be regarded as the culminating and leading feature of a course of botanical study."[69] That prophecy was not fulfilled in "a few years," but in 1902 V. M. Spalding, speaking before the Society for Plant Morphology and Physiology, still had high hopes:

> Modern science, favored as never before with the means of extension and development, should be able to justify its cost to the state by contributing to the betterment of human life. Tested by its capacity to meet this demand, ecology I think, will not be found wanting. Agriculture, horticulture and forestry are, consciously or not, practical applications of its principles, and their best development has been attained where these principles have been most intelligently observed and applied. It is safe to predict for all these great industries a growth in our country of which we can at present form but slight conception, and it is equally safe to say that as contributing to this development the study of ecology, now beginning to take definite and permanent form, will abundantly prove its necessity and value.[70]

Spalding was certainly correct about the growth of agriculture, horticulture, and forestry, but the science of ecology did not develop in close association with these practical pursuits. It would be many years before an ecological point of view would find its way into agricultural science, and the ecological work done during Spalding's day was of little practical value to the farmer. While utilitarian concerns may have provided an indirect stimulus for ecological investigations, most of the direct stimulus came from within the botany profession itself. The westward expansion, the corresponding rise and growth of state universities in the midwest, and the establishment of the Department of Agriculture and the agricultural experiment stations all contributed to the creation of many new positions for professionally trained botanists. The major taxonomic work connected with the expeditions into the western territories was nearing completion at the end of the nineteenth century. Meanwhile, the newer ideas from Germany were beginning to find their way into botanical instruction in America. Botany as an academic discipline reflected the general self-consciousness of American science that expressed itself in a drive to match the quality of European work. Attendant with this drive was the emphasis on process and experiment, which in the biological sciences manifested itself most clearly in the new physiology developing on the European continent. The emerging generation of professional botanists in the 1890s had been exposed to laboratory methods, to physiology, to the concept of the plant as a functioning organism. Plant ecology represented an extension of the physiological point of view to understanding the plant in its natural surroundings, with the background still provided by the general problem of adaptation. It was not so much a response to the needs of agriculture or to the recognition of the limitations of natural resources as it was a response to the professional development of the science of botany.

NOTES

1. *Proceedings of the Madison Botanical Congress* (Madison, Wisconsin, 1894), pp. 35[illegible] Robert C. Stauffer, "Haeckel, Darwin, and Ecology," *Quarterly Review of Biology* 32 (195[illegible] 138–44.

2. Bessey to MacMillan, November 17, 1899, Bessey Papers, University Archives, University of Nebraska, Lincoln.

3. *American Association for the Advancement of Science (AAAS) Proceedings* 53 (1903–04): 540–44.

4. For numerous examples of nineteenth-century ecological studies in America, see Frank N. Egerton, "Ecological Studies and Observations before 1900," in *Issues and Ideas in America*, ed. B. J. Taylor and T. J. White (Norman: Oklahoma University Press, 1976), pp. 311–51; reprinted in *History of American Ecology*, ed. F. N. Egerton (New York: Arno Press, 1977).

5. Roscoe Pound and Frederic E. Clements, *The Phytogeography of Nebraska*, 2nd ed. (Lincoln, Nebraska: The Seminar, 1900); H. C. Cowles, "The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan," *Botanical Gazette* 27 (1899): 95–117, 162–202, 281–308, 361–91.

6. This point of view concerning the central role of Clements and Cowles can be found throughout the literature in the history of American ecology, most of which has been written by ecologists. See, for example, Richard Brewer "A Brief History of Ecology: Part 1—Pre-nineteenth Century to 1919," *Occasional Papers of the C. C. Adams Center for Ecological Studies* 1 (1960): 1–17; Henry S. Conard, "Plant Associations on Land," *American Midland Naturalist* 21 (1939): 1–27; Robert P. McIntosh, "Ecology since 1900," in *Issues and Ideas in America*, pp. 353–72, reprinted in *History of American Ecology*; Hugh M. Raup, "Trends in the Development of Geographical Botany," *Annals of the Association of American Geographers* 32 (1942): 319–54; and Paul B. Sears, "Plant Ecology," in *A Short History of Botany in the United States*, ed. Joseph Ewan (New York: Hafner, 1969), pp. 124–31. The dominant role of Clements in America ecology is also discussed in recent works by historians, such as Ronald Tobey, "Theoretical Science and Technology in American Ecology," *Technology and Culture* 17 (1976): 718–28; Tobey, "American Grassland Ecology, 1895–1955: The Life Cycle of a Professional Research Community," in *History of American Ecology*; and Donald Worster, *Nature's Economy: The Roots of Ecology* (San Francisco: Sierra Club, 1977). It is not entirely correct to lump Clements's and Cowles's views together as I have done here. Both emphasized process and change, but Clements stressed the concept of the community as a superorganism, while Cowles was concerned more with the responses of plant populations to local environmental conditions. More mature statements of their views are found in Cowles, "The Causes of Vegetation Cycles," *Botanical Gazette* 51 (1911): 161–83; and Clements, *Research Methods in Ecology* (New York: Holt, 1905), and *Plant Succession* (Washington: Carnegie Institution, 1916).

7. David Hull, *The Philosophy of Biological Science* (Englewood Cliffs, N.J.: Prentice-Hall, 1974), p. 46. The contemporary plant ecologist is John L. Harper. See, for example, "A Darwinian Approach to Plant Ecology," *Journal of Ecology* 55 (1967): 242–70.

8. Michael Ghiselin, *The Economy of Nature and the Evolution of Sex* (Berkeley: University of California Press, 1974), p. 30.

9. For a general discussion of these issues, see Roderick Nash, *Wilderness and the American Mind* (New Haven: Yale University Press, 1967), and Joseph M. Petulla, *American Environmental History: The Exploitation and Conservation of Natural Resources* (San Francisco: Boyd & Fraser, 1977).

10. An examination of the ecological, as related to the physiological, orientation in late nineteenth-century botany, especially in Germany, is the subject of my dissertation in progress at the University of Wisconsin, Madison.

11. Exact figures regarding the growth of the botany profession in America are difficult to come by. William G. Farlow estimated that there were a half dozen botany professors in 1865, in "The Change from the Old to the New Botany in the United States," *Science* 37 (1913): 80. The Directories in the *AAAS Proceedings* list members of the Botanical Club and later Section G. Membership increased from 70 in the Botanical Club in 1885 to 125 in Section G by 1900, but probably less than half of these members were university professors and fewer still were agricultural researchers. An independent study by the editor of *American Men of Science* listed 53 botany professors in American universities in the year 1903—J. McKeen Cattell, "A Statistical

Study of American Men of Science: The Selection of a Group of One Thousand Scientific Men," *Science* 24 (1906): 659.

12. *Proceedings of the Madison Botanical Congress*, pp. 36-37.

13. Various aspects of the older methods of instruction are discussed in W. G. Farlow,"The Change from the Old to the New Botany," C. E. Bessey, "Some of the Next Steps in Botany," *Science* 37 (1913): 1-13, and E. A. Bessey, "The Teaching of Botany Sixty-Five Years Ago," *Iowa State College Journal of Science* 9 (1935): 227-33.

14. Raymond J. Pool, "The Evolution and Differentiation of Laboratory Teaching in the Botanical Sciences," *Iowa State College Journal of Science* 9 (1935): 237; Joseph Ewan, "Charles E. Bessey," *Dictionary of Scientific Biography (DSB)* (New York: Scribner's, 1970). A discussion of the "new botany" can be found in Andrew D. Rodgers, III, *American Botany 1873-1892: Decades of Transition* (Princeton: Princeton University Press, 1944); and A. Hunter Dupree, *Asa Gray* (New York: Atheneum, 1968), chapter 19.

15. "Botanical Instruction in this Country," *Science* 7 (1886): 251.

16. Charles E. Bessey, *Botany for High Schools and Colleges* (New York: Holt, 1880); Julius Sachs, *Lehrbuch der Botanik nach dem gegenwärtigen Stand der Wissenschaft* (Leipzig, 1868).

17. W. G. Farlow, "The Change from the Old to the New Botany," p. 84; review of Julius Sachs,*Text-book of Botany, Morphological and Physiological*, trans. A. W. Bennet and W. T. Thiselton Dyer (Oxford: Clarendon Press, 1875), in *American Naturalist* 10 (1876): 37-38.

18. Joseph Ewan, "Charles E. Bessey," *DSB*.

19. John M. Coulter, *Botanical Gazette* 5 (1880): 9; Asa Gray, *American Journal of Science* 120 (1880): 337; *American Naturalist* 14 (1880): 797-98.

20. W. G. Farlow, "Change from the Old to the New Botany," p. 85; Conway MacMillan, "On the Emergence of a Sham Biology in America," *Science* 21 (1893): 184-86. Letters in response to this article appear on pages 220, 234, and 287 of that volume; MacMillan's reply is on p. 289.

21. *AAAS Proceedings* 43 (1894): 237; "The Phylogenetic Taxonomy of Flowering Plants," *Annals of the Missouri Botanical Garden* 2 (1915): 109-64.

22. Bessey's association with agriculture and his relationship to the professionalization of botany are discussed at length in Richard A. Overfield, "Charles E. Bessey: The Impact of the 'New Botany' on American Agriculture, 1880-1910," *Technology and Culture* 16 (1975): 162-81. Ronald Tobey discusses the specific influences of the needs of the agricultural community on the ecological work of Bessey's students in "Theoretical Science and Technology in American Ecology."

23. Bryan D. Halsted, "Botany at the Washington Meeting," *American Naturalist* 25 (1891): 914. A more complete discussion of scientific research at the agricultural experiment stations can be found in Charles E. Rosenberg, "Science, Technology, and Economic Growth: The Case of the Agricultural Experiment Station Scientist, 1875-1914," *Agricultural History* 44 (1971): 1-20, reprinted in Rosenberg, *No Other Gods: On Science and American Social Thought* (Baltimore: The Johns Hopkins University Press, 1976), pp. 153-72; and in Reynold M. Wik, "Science and American Agriculture," in *Science and Society in the United States*, ed. D. D. Van Tassel and M. G. Hall (Homewood, Illinois: Dorsey Press, 1966), pp. 81-106.

24. J. C. Arthur, "Development of Vegetable Physiology," *Botanical Gazette* 20 (1895): 394.

25. W. G. Farlow, "The Task of American Botanists," *Popular Science Monthly* 31 (1887): 311-12.

26. Ibid., p. 305.

27. J. S. Burdon-Sanderson, "Presidential Address," *British Association for the Advancement of Science Report* 63 (1893): 12.

28. "Development of Vegetable Physiology," p. 391.

29. Ibid., p. 381.

30. Erwin F. Smith, "The First Annual Meeting of the Society for Plant Morphology and Physiology," *American Naturalist* 32 (1898): 96-97.

31. *Proceedings of the Madison Botanical Congress*, p. 36.

32. Ibid., pp. 37-38.

33. Patrick Geddes, *Chapters in Modern Botany* (London: John Murray, 1893), p. 22; W. F. Ganong, "The Term Phytobiology," *Botanical Gazette* 20 (1895): 38.

34. Unless otherwise indicated, the biographical information contained in this section is taken from *American Men of Science*, ed. J. M. Cattell, 1st, 2nd, & 3rd eds. (New York: The Science Press, 1906, 1910, 1921).

35. Merriam's theory of life zones is discussed at length in Keir B. Sterling, *Last of the Naturalists: The Career of C. Hart Merriam* (New York: Arno Press, 1974), and several of Merriam's articles on this subject have been reprinted in *Selected Works of Clinton Hart Merriam*, ed. & intro. Keir B. Sterling (New York: Arno, 1974).

36. F. V. Coville, "The Botany of the Death Valley Expedition," *Contributions to the U.S. National Herbarium* 4 (Washington, 1893).

37. Thomas H. Kearney "The Plant Covering of Ocracoke Island: A Study in the Ecology of North Carolina Strand Vegetation," and "Report of a Botanical Survey of the Dismal Swamp Region," *Contributions to the U.S. National Herbarium* 5 (1900): 263-319; and (1901): 321-585.

38. Frederick V. Coville and Daniel T. MacDougal, *The Desert Botanical Laboratory of the Carnegie Institution* (Washington: Carnegie Institution, 1903); D. T. MacDougal, "The Influence of Light and Darkness upon Growth and Development," *Memoirs of the New York Botanical Garden* 2 (1903); H. C. Cowles, "The Work of the Year 1903 in Ecology," *Science* 19 (1904): 882; D. T. MacDougal, *Botanical Features of North American Deserts* (Washington: Carnegie Institution, 1908); "Daniel Trembley MacDougal," *National Cyclopedia of American Biography* (New York: James T. White, 1931), 21: 42-43.

39. D. T. MacDougal, *Botanical Features*, p. 1.

40. Transcript, Student Records, 1873-1896, University Archives, University of Nebraska, Lincoln.

41. Additional biographical information for MacMillan was obtained from C. O. Rosendahl, "History of the Department," unpublished, Dept. of Botany Papers, Box 2, University of Minnesota Archives, Minneapolis, and from the Bessey-MacMillan correspondence in the Bessey Papers, University of Nebraska Archives, Lincoln.

42. Conway MacMillan, *The Metaspermae of the Minnesota Valley: A List of the Higher Seed-Producing Plants Indigenous to the Drainage Basin of the Minnesota River* (Minneapolis: Harrison & Smith, 1892); C. E. Bessey, *American Naturalist* 27 (1893): 365-66; MacMillan, "The Probable Physiognomy of the Cretaceous Plant Population," *American Naturalist* 27 (1893): 336-45; Bessey to MacMillan, 14 February 1893, Bessey Papers, University of Nebraska Archives.

43. Oscar Drude, "The Position of Ecology in Modern Science," trans. J. Patten, *International Congress on the Arts & Sciences, St. Louis, 1904* (Boston: Houghton-Mifflin, 1906), 5: 188.

44. "Observations on the Distribution of Plants Along Shore at Lake of the Woods," *Geological & Natural History Survey, Minnesota Botanical Series* 2 (1897): 949-1023.

45. *Minnesota Plant Life* (Minneapolis, 1899).

46. MacMillan to Clements, 3 January 1907, copy in Bessey Papers, University of Nebraska Archives.

47. F. E. Clements, review of *Minnesota Plant Life*, *American Naturalist* 34 (1900): 238-40; Raymond J. Pool, "Frederic E. Clements," *Ecology* 35 (1954): 109-112; Roscoe Pound, "Frederic Clements as I Knew Him," *Ecology* 35 (1954): 112-13; H. L. Shantz, "Frederic Edward Clements," *Ecology* 26 (1945): 317-19; A. G. Tansley, "Frederic Edward Clements," *Journal of Ecology* 34 (1947): 194-96.

48. Roscoe Pound, "The Plant-Geography of Germany," *American Naturalist* 30 (1896): 465-68; Drude, *Deutschlands Pflanzengeographie* (Stuttgart, 1896).

49. A. S. Hitchcock, review of Eugen Warming, *American Naturalist* 31 (1897): 435-40; "Oecological Plant Geography of Kansas," *Transactions of the Academy of Science, St. Louis* 8 (1898): 55-69.

50. Eugen Warming, *Plantesamfund: grundtrak of den ökologiska plantegeogrefi* (Copenhagen, 1895); *Lehrbuch der Oekologischen Pflanzengeographie: Eine Einführung in die Kenntnis der Pflanzenvereine*, trans. E. Knoblauch (Berlin, 1896); *Oecology of Plants: An Introduction to the Study of Plant Communities*, trans. P. Groom and I. B. Balfour (London: Oxford University Press, 1909).

51. H. C. Cowles, "The Physiographic Ecology of Chicago and Vicinity," *Botanical Gazette* 31 (1901): 73-108, 145-82; C. C. Adams and G. D. Fuller "Henry Chandler Cowles, Physio-

graphic Plant Ecologist," *Annals of the Association of American Geographers* 30 (1940): 39-43; William S. Cooper, "Henry Chandler Cowles," *Ecology* 16 (1935): 281-83.

52. H. C. Cowles, "Physiographic Ecology of Chicago and Vicinity," p. 79.

53. H. N. Whitford, "The Genetic Development of the Forests of Northern Michigan: A Study in Physiographic Ecology," *Botanical Gazette* 31 (1901): 289-325; Edgar N. Transeau, "On the Distribution and Ecological Relations of the Bog Societies of Northern North America," *Botanical Gazette* 36 (1903): 410-20; and "Forest Centers of Eastern American," *American Naturalist* 39 (1905): 875-89.

54. John W. Harshberger, "An Ecological Study of the Flora of Mountainous North Carolina," *Botanical Gazette* 36 (1903): 241-58, 368-83; "An Ecological Study of the New Jersey Strand Flora," *Proceedings of the Academy of Science Philadelphia* 52 (1900): 623-71; 54 (1902): 642-69; *Phytogeographic Survey of North America* (New York: G. E. Stechert, 1911).

55. V. M. Spalding, "The Rise and Progress of Ecology," *Science* 17 (1903): 201-10; H. S. Reed, "A Survey of the Huron River Valley I: The Ecology of a Glacial Lake," *Botanical Gazette* 34 (1902): 125-39; L. H. Weld, "Botanical Survey of the Huron River Valley II: A Peat Bog and Morainal Lake," *Botanical Gazette* 37 (1904): 36-52; H. S. Reed, "A Brief History of Ecological Work in Botany," *Plant World* 8 (1905): 163-71, 198-208.

56. W. F. Ganong, "Beiträge zur Kentniss der Morphologie und Biologie der Cacteen," Ph.D. thesis, published in *Flora* 79 (1894): 49-86; Karl Goebel, *Pflanzenbiologische Schilderungen* I (Marburg, 1889). Biographical information for Ganong was obtained from *William Francis Ganong Memorial*, ed. J. C. Webster (Saint John: New Brunswick Museum, 1942; rprt. 1967).

57. W. F. Ganong, "Present Problems in the Anatomy, Morphology, and Biology of the Cactaceae," *Botanical Gazette* 20 (1895): 132.

58. W. F. Ganong, "An Outline of Phytobiology," *Bulletin of the Natural History Society of New Brunswick* 3 (1894): 3-15.

59. (New York: Holt, 1901).

60. Ganong was an ardent woodsman. His "New Brunswick Journals" contain field notes gathered on no less than 106 separate trips, many of them several weeks in length, between 1880 and 1929. Archives, New Brunswick Museum, Saint John, N.B.

61. W. F. Ganong, "The Vegetation of the Bay of Fundy Salt and Diked Marshes: An Ecological Study," *Botanical Gazette* 36 (1903): 161-86, 280-302, 349-67, 429-55; H. C. Cowles, "The Work of the Year 1903 in Ecology," p. 883.

62. J. R. Green, *A History of Botany, 1860-1900; Being a Continuation of Sachs' 'History of Botany, 1530-1860'* (Oxford: Clarendon Press, 1909), p. 494.

63. *Phytogeography of Nebraska*, p. 161.

64. F. E. Clements, *Research Methods in Ecology*, p. 1; H. C. Cowles, "An Ecological Aspect of the Concept of Species," *American Naturalist* 42 (1908): 265.

65. *Proceedings of the Madison Botanical Congress*, p. 36; H. C. Cowles, "Work of the Year 1903 in Ecology," p. 79.

66. W. F. Ganong, "The Cardinal Principles of Ecology," *Science* 19 (1904): 493-94.

67. W. F. Ganong, "An Outline of Phytobiology," p. 4.

68. *Proceedings of the Madison Botanical Congress*, p. 37.

69. "Development of Vegetable Physiology," p. 394.

70. "The Rise and Progress of Ecology," p. 209.