However, when he discussed the *processes* that occur in communities and ecosystems, Whittaker often slipped back into more organic or physiological descriptions: populations were parts of a larger whole, and each played a specific functional role to maintain the integrity of that whole.[56]

Much of Clementsian ecology has not stood the test of time. His continued belief in the inheritance of acquired traits, long after it was rejected by most other biologists, was aberrant. His mechanistic notions of cause and effect were considered simplistic even by many of his contemporaries. His insistence that succession is always progressive was also rejected by many ecologists of his day. His ideas of climax and the organic unity of the community were more influential, but they too have been modified or abandoned. Yet, despite all this, Clementsian thought has been enormously influential. As even his critics admitted, the very scope and systematic nature of Clements's work integrated ecological thought, and it stimulated both further research and criticism.[57] More important, Clements emphasized the importance of process in ecology, and he suggested a useful physiological perspective for studying it. This had a powerful influence on the development of ecology.

Few ecologists after World War II believed that a community or ecosystem really was an organism, but in important ways they continued to believe that these higher level systems behaved somewhat like organisms. Succession was the paradigmatic example. Although the Clementsian explanation was wrong in its details, the general idea that succession is a developmental process continued to serve as an important heuristic argument and a useful framework for explanation.[58] The physiological perspective suggested other important analogies between organisms and higher level systems. After World War II ecosystem "metabolism" and "homeostasis" became important areas of ecological research. Clements never considered these ideas, but they fit neatly into his general view that ecology was to be "a rational field physiology."

3

An Ambiguous Legacy

One's success as a scientist can be measured more by the number of people he or she puts to work on new problems than by the correctness of specific research results.

—DAVID M. RAUP, *The Nemesis Affair*

The man who states a general theory which leads subsequent workers along the most fruitful lines of research performs a service which is fundamental to the progress of science.

—A. G. TANSLEY, "Frederic Edward Clements, 1874–1945"

FREDERIC CLEMENTS is an enigmatic historical figure. Universally recognized as one of the founding fathers of ecology, he has, nonetheless, become a convenient "fall guy" for some modern ecologists.[1] During his lifetime Clements's opponents ridiculed his ideas by characterizing them as "flights of fancy," "fairy tales," and "laughable absurdities."[2] Yet much to the consternation of modern critics, these same Clementsian ideas persist in modified form today.[3] How can one explain this ambiguous legacy? The story of the Clements-Gleason controversy, so popular among ecologists today, provides few insights. Indeed, the answer to this question is not found in intellectual comparisons removed from social context. The ambiguities surrounding Clements's historical reputation are better explained by considering the fate of the research group that he formed during the second decade of the twentieth century.

In its details, Clementsian ecology was badly flawed. But being wrong, perhaps even being egregiously wrong, is not antithetical to good science. Most scientists are wrong most of the time, and even great scientists turn out to be wrong much of the time. What is really important in science is identifying an important problem or proposing a fruitful set of ideas that then become the roots for a new line of research. Often, as this new intellectual lineage develops, the original ideas are refined, modified, or replaced. Historians, sociologists, and philosophers have emphasized the important role that small groups of interacting scientists (i.e., research schools or research groups) play in this developmental process.[4] The research group provides an established scientist with an array of resources that greatly expands the scope of scientific work. It also provides the scientist with a potential means for promoting the development of original ideas. To the extent that a scientist can successfully recruit bright young workers, committed to a particular line of research, he or she can establish an intellectual tradition. Failing this, a scientist's ideas are at the mercy of the broader scientific community, where they are frequently ignored. Even if they prove influential, without an active research group to nurture the growth of nascent ideas the scientist has little control over how other independent scientists will interpret and modify these ideas.

Clements's association with the Carnegie Institution of Washington dramatically illustrates both the potential resources provided by the research group and the problems of fully exploiting these resources. His career demonstrates the way that personality can interact with intellectual and political factors in determining the fate of a line of research. The Carnegie provided Clements with great potential resources, both financial and institutional. He skillfully used these to promote his ecological ideas, and these ideas influenced many ecologists. But Clements was less successful in establishing an effective, enduring research group at the Carnegie. For the most part, the younger scientists who joined him did not expand upon his most suggestive ideas. The Clementsian research group did not survive its leader, and later in his career Clements's thinking became increasingly idiosyncratic; the development of his older ideas came primarily from the work of scientists unassociated with the Carnegie Institution. Thus the ambiguity arises: Clementsian ecology was influential, but, although criticized for errors in his thought, he rarely receives credit for later innovations that sprang from his original ideas.

Clements and the Carnegie Institution

The Carnegie Institution of Washington was established in 1902 with an endowment of $10 million from steel magnate Andrew Carnegie.[5]

However, compared to the Rockefeller Institute, the other great supporter of American science during this period, the funding policies of the Carnegie Institution were rather nebulous. During the early decades of its existence the institution supported a wide variety of research projects, and there was considerable debate within the institution over the relative merits of various intellectual fields.[6] One field that received early and enduring support was botany, beginning with the establishment of a desert laboratory near Tucson, Arizona, in 1903.[7] During the next several decades botanical research supported by the Carnegie Institution expanded into a number of other areas including evolution, physiology and biochemistry, ecology, genetics, taxonomy, and paleontology.

During this formative period in its history Frederic Clements became associated with the Carnegie Institution. In 1903 he approached the institution for financial support with a request for eight hundred dollars to purchase instruments for his ecological studies on Pikes Peak.[8] Frederick Coville, a research associate at the Desert Laboratory who reviewed the proposal, was impressed with both Clements's proposed research and his qualifications as a scientist. However, citing the uncertainty in the institution's plans for botanical research he recommended deferring the award. "It is believed that the application should ultimately be granted," Coville wrote, "but that it would be advisable to defer the grant until a plan has been adopted by the Institution for the coordination of the researches bearing on this [ecological] subject."[9] Not until nearly a decade later did the Carnegie Institution begin to support Clements's ecological research. During the intervening years he established an international reputation with the publication of *Research Methods in Ecology* (1905) and was appointed chairman of the botany department at the University of Minnesota. In 1913 Clements took a six-month leave of absence to work at the desert laboratory. During the next three years the Carnegie Institution supported his research with small grants, and following the completion of his greatest work, *Plant Succession* (1916), Clements was appointed full-time research associate, a position that he held until his retirement in 1941.[10]

Clements joined the Carnegie Institution at a propitious time for program building. Not only did botanical research expand there throughout the 1920s, but the institution was also attempting to organize this research around evolution, development, and physiology—precisely the major themes of Clementsian ecology. Clements seemed to possess the characteristics necessary to play a central role in this reorganized botanical program. Under the presidency of Robert

S. Woodward (1904–1920) the funding policy of the Carnegie Institution of Washington had shifted away from small grants-in-aid and toward long-term funding of a few "exceptional men" whose research was central to well-established scientific fields.[11] Clements had established himself as a respected leader in the young discipline of ecology. *Plant Succession*, which was in the process of being published by the institution when Clements's research associateship was under discussion, promised to be a work of major significance. In his presidential report of 1916, Woodward extolled it as a "remarkable" and "profoundly instructive" book dealing with the central problems of ecology and evolutionary biology.[12] Woodward was not the only administrator impressed with Clements's intellectual abilities. Daniel Trembly MacDougal, director of the Department of Botanical Research and a man with a keen political sense, was also an enthusiastic backer. MacDougal had been instrumental in bringing Clements to the Carnegie, and his support seemed to bode well for Clements's future within the institution.

In his letter of appointment, Woodward wrote Clements that he wished to use the ecologist as an example of what it meant to be a full-time associate of the Carnegie Institution.[13] First, only scientists of the highest caliber would be considered for such positions. Second, in terms of salary and security, the institution was willing to offer its associates benefits equal to those enjoyed by full professors at leading universities. Perhaps most important for Clements's ambitious plans for the future, the letter suggested that his status within the institution would be equal to that of the director of a research department; thus, Clements would be able to hire a team of scientists to work under his direction. For a decade after Clements joined the institution his research group in ecology continued to enjoy this informal, quasi-departmental status.

Clements realized, however, that without formal departmental status there was a danger that he would lose control over ecological research, a fear borne out by later events. Therefore, almost immediately after joining the Carnegie Institution, Clements began lobbying for a separate department of ecology. In a memorandum to Woodward written in 1919, he outlined a comprehensive scheme for such a department. This outline faithfully reflected the conceptual framework presented in *Research Methods in Ecology* fifteen years before, with the notable addition of animal ecology as an important element in the program. Clements would direct this program in "pan-ecology" or "bio-ecology." Subdivided into four areas, each had its own permanent research associate: *experimental taxonomy* would investigate the evolutionary relationships among species; *experimental ecology* would study physiological adaptations in individual plants; *experimental vegetation* would extend Clements's earlier studies on the dynamics of plant communities; and *experimental biology* would investigate the ecological interactions between plants and animals. To carry out this ambitious research program Clements asked for four primary investigators, two full-time assistants, four or five part-time assistants, a secretary, and an annual budget of $34,000.[14] At a time when automobiles could be purchased for less than $500, this was no small sum. Clements eventually received most of his request, but Woodward was decidedly cool to his idea of a separate department for ecology. The economic uncertainty of the immediate post–World War I period was an important reason for Woodward's reticence, as perhaps was the fact that he was planning to retire as president. There were other important reasons for not supporting Clements's proposed department, reasons that Woodward did not articulate. One was the conservatism of the Carnegie Institution. In general, the institution supported research in well-established fields and avoided committing itself to novel ventures.[15] Clements's ecological research was acceptable within the broader intellectual context of botany, but as an independent field ecology was still struggling to establish an identity. An equally important reason for rejecting Clements's proposal was opposition from other biologists at the Carnegie Institution.

During the 1920s the Carnegie Institution was an intensely competitive arena, with many ambitious scientists jockeying for influence and control over institutional resources. Those less adept at internal politics could find their status within the institution greatly diminished. In her biography of Forrest Shreve, Janice Bowers has carefully documented the professional stumbling blocks that even talented scientists faced at the Carnegie. Shreve was a gifted botanist but not an astute "biopolitician."[16] Consequently his prestige within the institution suffered, and eventually his research program was eliminated. Clements's case was somewhat different: initially he had tremendous respect within the institution, and he was extremely ambitious. Although much more successful than Shreve, Clements's position within the institution also eroded over the years, a decline explained by the interplay between personalities and intellectual agendas.

Photographs of Clements invariably show an intensely serious individual (figure 2). Ecology was an obsession, and by midcareer the pressures of research had driven him to physical and emotional exhaustion.[17] Puritanical in personal habits, he abstained from tobacco and alcohol and was distressed by colleagues who did not. He was aloof, arrogant, and intellectually inflexible. Although flashes of humor occasionally appear in his correspondence, they seem strained and out of character. Even in Edith Clements's light-hearted memoir, *Adventures in Ecology* (1960), her late husband consistently comes off as a cold fish.

Character flaws do not preclude scientific creativity, but they can be professionally detrimental. Many scientists found Clements a difficult man to work with, and this affected his ability to direct a successful research group. Even before joining the Carnegie Institution, his prickly personality had almost derailed his career. Clements's first important professional break came in 1907 when he was appointed chairman of the Department of Botany at the University of Minnesota. Previously he had been teaching at his alma mater, the University of Nebraska. Clements was apparently not popular at Minnesota, and initial opposition to his appointment there was intense. Opponents presented the president and board of regents with a long list of complaints about the candidate's personality. These ranged from serious—that Clements was difficult to get along with and would lead to disharmony within the department—to scurrilous—insinuations that he and Edith Clements were not legally married. Critics suggested that he was being highly recommended only because the University of Nebraska wanted to get rid of him. Charles Bessey, Clements's mentor at the University of Nebraska, was sufficiently concerned about these charges that he composed a five-page letter rebutting each complaint against his former student.[18] When finally offered the position after a protracted search, Clements acknowledged that he was fortunate to get it, and he hoped that the department would "sooner or later feel the same way about their side of the bargain."[19] Clements chaired the department for a somewhat stormy decade, and the difficulties that his appointment faced at the University of Minnesota foreshadowed problems that he encountered later at the Carnegie Institution.

As botanical research at the Carnegie Institution expanded and diversified, Woodward and his successor as president, John C. Merriam (1920–1938), attempted to reorganize the program in a way that encouraged cooperation among researchers and simplified the administration of botanical work being carried out at several laboratories.[20] Eventually this led to the formation of a Division of Plant Biology with its headquarters on the campus of Stanford University.[21] However, the establishment of this new research unit came only after a decade of debate and negotiation within the Institution. Throughout the 1920s, Clements continued to campaign for a department of ecology, but other suggestions for reorganizing botanical research at the Carnegie Institution were also presented, some in direct opposition to Clements's ideas. Not only was this opposition partly personal and political, but it also reflected sharply divergent perspectives on the future course of botanical research.

Throughout the process of reorganization the administration placed great emphasis upon the necessity of coordination, cooperation, and efficiency in scientific research.[22] Implementing such lofty goals, however, among a diverse group of independent scientists was a major problem. Clements, with his domineering personality and single-minded commitment to ecology, was unlikely to encourage cooperation from other specialized botanists. From the beginning of his career, Clements had conceived of ecology as "the dominant theme in the study of plants, indeed, as the central and vital part of botany."[23] This grandiose view of ecology continued to inform Clements's plans for reorganization during the 1920s. In Clements's later schemes, all botanical research at the Carnegie Institution would cohere around an ecological theme, and other researchers appeared to be little more than subordinates in Clements's larger ecological research program.[24] Under any circumstances such a centralized research program could not have been very appealing to other prominent botanists at the Carnegie. The plan was even less appealing given the controversial nature of some aspects of his research, particularly as it applied to physiology and genetics. Indeed, even without his abrasive personality, Clements probably would have come into conflict with the Carnegie physiologists and geneticists for purely intellectual reasons.

Clementsian ecology, first outlined in *Research Methods in Ecology* (1905), was based upon the premise that both individuals and communities are organisms, and as such they share fundamental physiological properties. As a broad approach to ecological research, this physiological perspective was extremely suggestive, but many of Clements's specific claims about physiological cause and effect were naive. Traditional laboratory physiologists ridiculed him. In an extremely negative review, Charles Barnes, a physiologist at the University of Chicago, decried Clements's "vague explanations" and his "invalid reasoning."[25] Burton Livingston, a physiological ecologist at the Johns Hopkins University and a research associate at the Carnegie, dismissed *Research Methods* as "that *awful* book."[26] The book fared better with two British critics: the ecologist Arthur Tansley and the physiologist F. F. Blackman.[27] Although they wrote a long, generally laudatory review of *Research Methods*, correspondence suggests that the two reviewers were not equally enthusiastic about the book.

In a letter to Tansley, Blackman admitted that Clements's broad physiological approach to ecology was intriguing, but he was "repelled" by the details.[28] Criticism of his physiological approach to ecology followed Clements to the Carnegie. H. A. Spoehr, who eventually became the director of the new Department of Plant Biology in 1929, shared the disdain of other physiologists toward Clements's work. Spoehr was just as ambitious as Clements, and their relationship was generally hostile. Through private correspondence with President Merriam, Spoehr criticized the physiological work done in Clements's laboratory in an attempt to undermine the credibility of his research program.[29]

Clements's attitude toward genetics and his relationship with the geneticists at the Carnegie Institution was more complex. From the beginning, he believed in the inheritance of acquired traits and was convinced that speciation sometimes occurred by this process within a few generations.[30] Within the context of early twentieth-century botany this claim was controversial but legitimate, and inheritance of acquired traits fitted neatly into Clements's plans for an ecology based upon experimentation. By manipulating the environments of plants the botanist might be able to mimic the evolutionary process. This experimental taxonomy was a major part of his research program, and it increasingly dominated Clements's attention later in his career. During the early years of the twentieth century, such evolutionary views were within the mainstream of biological opinion, and the Carnegie Institution had a tradition of supporting research on the inheritance of acquired traits. Daniel Trembly MacDougal, who established the botany program at the Carnegie, was a prominent neo-Lamarckian. Even as late as 1925 other botanists associated with the institution, including the geneticists E. B. Babcock and A. F. Blakeslee, were willing to concede that Clements's experimental taxonomy was legitimate, perhaps even important, scientific research.[31] For example, in a long letter to President Merriam, Blakeslee wrote:

> The problem of the experimental induction of genetic change (mutations, heritable variations) in other words of experimental evolution is an alluring one to all biologists + has been the definite aim of the geneticist as indicated by the name of our Station at Cold Spring Harbor [Station for Experimental Evolution]. It must be admitted, however, that despite the enormous amount of thought + experiment on the problem, the most of which [*sic*] is unpublished, there is no single case during the last quarter of a century accepted by geneticists as an induction of a strictly genetic change.[32]

Blakeslee outlined the rigorous experimental conditions that needed to be met before geneticists would accept the validity of Clements's neo-Lamarckian claims. Despite his skepticism, however, Blakeslee expressed a willingness to cooperate with Clements on evolutionary studies.[33]

During the period of reorganization at the Carnegie Institution, Clements's commitment to neo-Lamarckism began to harden, and probably concern over his declining influence within the institution (discussed below) contributed to this change in his attitude. In August 1928 Clements wrote Merriam,

> It has now become possible to convert several Linnean species into each other, histologically as well as morphologically, and I need your judgment and advice as to kinds of evidence and the best methods of presentation. Both technique and results have reached the point where it should be possible to set the stage for a comprehensive demonstration within the next two or three years.[34]

Given the earlier discussions within the institution about experimental evolution, Merriam was greatly intrigued by Clements's claim, and he suggested that Clements present his preliminary findings before a conference of Carnegie biologists.[35] Whatever his motivation for writing to Merriam, Clements unfortunately did not have the data to back up his claim, and thus he had placed himself in an extremely awkward position. He was forced to delay presenting his results, a tactic that he continued until the end of his life. Perhaps anxiety over his position within the institution contributed to his increasingly anachronistic ideas about evolution. By the end of the 1920s he realized that his prestige within the Carnegie had seriously eroded, and he voiced concerns about the political maneuvering and intrigue surrounding the reorganization of botanical research at the institution.[36] Whatever the reason, Clements's experimental studies on the inheritance of acquired traits became an embarrassment for the Carnegie Institution, and after his death the Institution refused to publish the results of this research.[37]

The shifting balance of power within the Carnegie Institution during the 1920s is perhaps best illustrated by the changing relationship between Clements and his colleague, Harvey Monroe Hall. Hall was a professor of botany and curator of the herbarium at the University of California when he joined Clements's research group at the Carnegie Institution in 1919.[38] During the next decade the two men collaborated on transplant experiments, a venture that led to an influential but controversial book, *The Phylogenetic Method in Taxonomy*.[39] The personal relationship between Clements and Hall was cordial, but their working relationship was never particularly close. They did some field research together, but Hall continued to work primarily at Berkeley, while Clements did most of his experimental transplants on Pikes Peak. Intellectually, too, the experimental taxonomists diverged. Hall, believing that experimental taxonomy was a method for studying evolutionary patterns and mechanisms in general, never embraced Clements's neo-Lamarckian views. Furthermore, Hall was much more willing than Clements to expand experimental taxonomy to include genetics and cytology, and, unlike Clements, he developed a close relationship with the geneticists at the Carnegie Institution. One of Hall's closest friends was the geneticist E. B. Babcock. Beginning in the early 1920s, while Hall was still a member of Clements's research group, he and Babcock began exploring the possibility of combining ecological, taxonomic, and genetic methods to study the evolutionary relationships among plant species.[40]

Hall's synthetic approach to botanical research and his ability to work closely with a variety of other specialists were apparently exactly what the administration of the Carnegie Institution had in mind when they called for cooperative research. In contrast to Clements's idea of botanical research dominated by his own ecological research program, Hall's plan called for a much looser collaboration among botanists; independent researchers would continue their individual projects, but they would meet periodically in a "research conference" to explore areas of common interest.[41] This plan did not become the exact blueprint for the reorganization of botanical research, but Hall did become increasingly influential within the Carnegie Institution. Beginning in 1926, control of experimental taxonomy began shifting from Clements to Hall, and after 1928 Hall directed an independent research group that eventually refuted Clements's neo-Lamarckian claims.[42] Perhaps more important, President Merriam appointed Hall, Spoehr, and Blakeslee to an advisory committee on the reorganization of botanical research. Clements was excluded from the decision-making process, and the recommendations of the committee undercut his authority. Despite protests from Clements, the headquarters for the new Department of Plant Biology was built on the campus of Stanford University, not at Clements's winter laboratory at Santa Barbara. Spoehr, who held Clements in low esteem, was appointed chairman. Clements's research program, which had enjoyed quasi-departmental status for nearly a decade, was now simply one unit within the larger Division of Plant Biology. The budget for ecological research was now under Spoehr's control, an arrangement Clements bitterly resented.[43] An important part of the Clementsian research program, experimental taxonomy, was completely removed from his control, and during the 1930s both the scope and the staffing of his ecological research were further eroded.[44] By the time of his retirement in 1941, Clements's program in ecology amounted to little more than his studies on inheritance of acquired traits.[45]

Building a Research Group

Political skirmishes notwithstanding, the Carnegie Institution provided Clements with an enviable set of resources for building a dynamic research group. Financial support for his program was modest in comparison to some larger biological departments in the institution, but few ecologists during the 1920s were supported as lavishly as Clements. Within the restrictions set by his budget, Clements was completely free to build a research group as he desired.[46] The number of biologists working with Clements varied, but during the 1920s the research group was generally composed of four or five scientists working under his direction. Being a research associate at the Carnegie also allowed Clements to devote all his efforts to research. As his wife put it, after 1917 Clements was an "escaped professor."[47] The associateship freed Clements from the burdens of teaching, but it did not isolate him from academia. Students from the University of Nebraska could earn academic credit for fieldwork done at Clements's alpine laboratory in Colorado, and a steady stream of young scientists from other universities visited the facility.[48] From the beginning, Clements recognized that the prestige of a research program depended upon the "constant output" of articles and books.[49] He was a prolific writer, and his publications undoubtedly would have been influential under any circumstances. But the Carnegie Institution provided Clements with various outlets for publishing the results of his research. In particular, Clements effectively used the institution's monograph series to present extensive, detailed reports of his various research projects. *Plant Succession* (1916), his most influential work, was part of the series. And during the decade of the 1920s the Carnegie published seven other large monographs written by Clements and his coworkers.[50]

In a competitive scientific environment, Clements had an extraordinary set of potential resources for developing and disseminating his ecological ideas. Initially, these resources were used effectively, and much of Clements's influence on ecology can be attributed to the institutional niche that he exploited at the Carnegie during the 1920s. Owing to the interaction of a number of factors only partially under his control, Clements, however, was unable to create a dynamic research group that could survive after his retirement.

One key ingredient for the success of a research group is effective leadership. A leader must be capable of recruiting subordinates who are not only sufficiently committed to the leader's research to remain loyal to the program but also sufficiently independent to further develop the leader's ideas, produce conceptual or methodological innovations, and expand the research program into new areas. It may be difficult to strike the right balance between loyalty and intellectual independence; not surprisingly, even very productive research groups may be rather volatile.[51]

Clements was quite successful in attracting devoted younger biologists to his research group, some of whom stayed with him throughout his career. But given his domineering personality, Clements's coworkers found it difficult to develop independent lines of research within the broader context of Clementsian ecology. Group members seemed to be faced with only two options: subordinate their research completely, or break with the team. John Weaver and Harvey Monroe Hall, two examples of successful biologists who worked with Clements, illustrate this dilemma.[52]

John Weaver was not a great scientist, but he had a long and productive career as a botanist at the University of Nebraska. He served as president of the Ecological Society of America, and at the time of his death in 1966, he was recognized as the foremost authority on the ecology of North American grasslands.[53] Weaver was one of several Ph.D.s trained by Clements at the University of Minnesota. After completing his degree in 1917, Weaver joined the faculty at Nebraska, and during the summers he worked as a member of Clements's research group.

Weaver's major professional problem was his inability to successfully sever his student-professor relationship with Clements. Throughout their correspondence, including letters written two decades after Weaver completed his Ph.D., Clements's salutation was "Dear Weaver" while Weaver invariably opened his letters with a more respectful "Dear Dr. Clements."[54] These very different salutations indicate the subordinate position that Weaver continued to hold vis-à-vis his former teacher. From Clements's point of view, Weaver's research was simply part of the larger "organic whole" of the Clementsian research program.[55] Not only did he dictate the substance of

Weaver's work, which continued Clements's earliest interests in the ecology of the Nebraska prairies, but he also meddled in the younger scientist's professional life. On two occasions, Clements pressured Weaver to withdraw manuscripts that had been accepted for publication in the *Botanical Gazette*.[56] The reason was transparently obvious; Clements wanted Weaver's work to appear in Carnegie publications, thereby enhancing the status of his ecology program within the institution.

Clements originally planned to have Weaver become a full-time member of his research group, an offer that Weaver ultimately rejected.[57] Weaver's reticence was based upon several factors, including the financial security, access to graduate students, and equipment that his position at the University of Nebraska provided. But Weaver may also have been aware that to advance professionally he needed to free himself, however imperfectly, from Clements's domineering personality. Looking at Weaver's career, we see a scientist who was highly committed to Clementsian ecology; yet he did not have the independence to expand significantly the scope of this research tradition. Though competent, and even technically innovative, Weaver's research during the 1920s and 1930s remained thoroughly wedded to Clements's early views on plant ecology.

The experience of Harvey Monroe Hall provides an interesting contrast with that of Weaver. Unlike most other members of Clements's research group, Hall, having earned his Ph.D. at the University of California, was an outsider with no ties to either Nebraska or Minnesota. Hall and Clements were the same age, and by the time the Californian joined the team in 1919 he had already established his reputation as a plant taxonomist. To a much greater extent than any other member of the group, Hall was Clements's coequal. Significantly, Hall was the only member of the team to appear as senior author on a major publication written with Clements.

Hall left the botany department at the University of California to join Clements's research group, but only after protracted negotiations. Like Weaver, he was concerned about losing the security of a faculty position. In most cases, the Carnegie Institution made no formal commitments to Clements's coworkers; they were hired by Clements and served at his pleasure. Presumably, if Clements were to leave, the institution would not continue supporting the research group. But part of Hall's reticence was also intellectual; he and Clements approached scientific research very differently. "You are naturally radical and ready to take chances," Hall wrote Clements in 1918. "I am naturally conservative and want to carry the public with us. You are so anxious to get our results into immediate use that the early issuance of popular manuals is an important part of your program; I also want to serve in this manner but anticipate more keenly the intensive and detailed systematic studies in herbarium, garden, and field."[58] Hall was concerned as much with substance as with style, and throughout his life he remained noncommittal toward many of Clements's theoretical claims. In particular, he distanced himself from Clements's enthusiastic neo-Lamarckism.[59]

In contrast to Weaver and other members of Clements's research group, Hall maintained a high degree of scientific independence. He continued to live and work near Berkeley, and he forged strong ties with geneticists during the years when Clements was beginning to alienate them. Significantly, however, Hall did expand part of the Clementsian research program. He took one of Clements's earliest and most fruitful ideas, experimental taxonomy, and further developed it in a novel way. Clements had envisioned this line of research as a hybrid between ecology and taxonomy, using transplant experiments to determine phylogenetic relationships among species. Hall greatly expanded this interdisciplinary area of research to include not only ecology but also genetics and cytology. But Hall's innovation came at Clements's expense: During the administrative shake-up of 1928, research in experimental taxonomy was removed from Clements's control and placed under Hall's supervision. This was the only part of Clements's original research program that survived after his retirement in 1941. Ironically, the new team that Hall assembled beginning in the late 1920s—Jens Clausen, David Keck, and William Hiesey—effectively disproved Clements's neo-Lamarckian claims.[60]

The cases of John Weaver and Harvey Hall illustrate an important weakness in Clements's program of research. Clements built a productive research group, but this team did not successfully develop many key concepts that Clements had suggested in *Research Methods in Ecology* (1905). Most members of the group—Weaver, Herbert Hanson, Frances Long, and Glenn Goldsmith—worked on rather narrow empirical problems.[61] None of these biologists used Clements's conceptual framework as a foundation for developing bold, innovative ecological theories. Hall, who successfully exploited one of Clements's broader theoretical claims, did so in a manner detrimental to Clements's program, both institutionally and intellectually. Ironically, Clements's most suggestive claims—that the community is a kind of organism with its own distinctive physiology and that succession is a developmental process—remained relatively undeveloped. These ideas did not disappear when Clements died. Their further elaboration, however, came not from his students or the members of his research group, but from ecologists unaffiliated with the Carnegie Institution of Washington.

Clements's Influence on Modern Ecology

Critics have often claimed that Clements's influence was so pervasive that it amounted to a kind of intellectual stranglehold on ecology. Only after his death, it is argued, did ecologists free themselves from the misguided Clementsian paradigm.[62] This idea of the rise and fall of Clementsian orthodoxy is historical myth. During his lifetime, his ideas were the subject of vituperative attacks, particularly by some European ecologists. Even in the United States and Britain, supposedly the strongholds of Clementsian ecology, most of Clements's specific claims about communities and succession were challenged by prominent ecologists.[63] Among the first rank of Anglo-American ecologists it is difficult to find a single individual who might accurately be characterized as an orthodox Clementsian. Even within his own institution Clements was an embattled biologist. This is not to claim that he was uninfluential. To the contrary, Clements's ideas formed an important part of the foundation for ecosystem ecology. But his modern critics have distorted the historical context within which these formative ideas developed. The true significance of Clements's work was not that his ideas were accepted as a kind of orthodoxy, but that other ecologists considered them sufficiently important to criticize, modify, and use as the basis for further work.

Ironically, the significance of Clements's work is most apparent in his erroneous views. Before considering these views, it may be useful to consider a taxonomy of scientific error. Scientists are frequently wrong, and their errors, once discovered, often have little impact on the future course of science. But scientific errors may also play a more positive role. By vociferously arguing for an alternative explanation, even if it turns out to be wrong, a scientist may force opponents to clarify ambiguities in their thinking and make their assumptions more explicit. Richard Goldschmidt, who was wrong more often than he was right, may have played this role of gadfly in the history of genetics.[64] The case of V. C. Wynne-Edwards and his theory of group selection is another excellent example. Although quickly rejected, this theory stimulated considerable discussion of evolutionary mechanisms, and thus it played an important role in the emergence of evolutionary ecology during the 1960s.[65] A different situation arises when a scientist proposes a broad, superficially appealing generalization that can be shown to be false in the details. Despite serious problems the idea may stimulate further research, and a modified version may eventually become widely accepted. The case of Alfred Wegener's theory of continental drift is a notable example of a problematic concept that later gained acceptance.[66] Conversely, a broad generalization that initially appears plausible may later be discredited. Yet the controversy that leads to the rejection of the concept may, in itself, stimulate the development of an area of research. J. C. Willis's theory of "age and area" in plant geography may be an example of this type of fruitful scientific error.[67]

Clements's mistaken views fall into each of these four broad categories. The results of his research on inheritance of acquired traits were virtually ignored by other biologists by the time they were posthumously published in 1950. His unorthodox ideas had no discernable effect on the development of evolutionary biology. His claim that succession is always a linear process, progressing toward a uniform climax, was widely rejected during his lifetime. Because, however, this claim was presented in *Plant Succession*, the definitive work on the subject, it could not be ignored. His dogmatic assertions forced other ecologists to distinguish more carefully among various types of succession: primary and secondary, allogenic and autogenic. Clements's intransigence undoubtedly annoyed his contemporaries, but it seems likely that in the development of theories of succession Clements played an important role as gadfly. Similarly, his sweeping generalizations about climax vegetation later served as a foil for criticism.[68] Clements's most basic claim—that the community is a kind of organism with its own physiology—was erroneous in a more interesting way. The concept was never fully developed by either Clements or his coworkers; his discussions of the concept at the end of his career barely differed from the one presented in *Research Methods in Ecology* (1905). After World War II few, if any, ecologists accepted the strong version of Clements's organismal concept, but in a weaker form this concept was tremendously fruitful. As we shall see, the idea of the ecosystem was a direct descendent of the organismal concept. If later ecologists denied that ecosystems were organisms, then they continued to compare the physiology of organisms and the "physiology" of ecosystems. Thus Clements's broad physiological perspective and organismal concept played important roles in initiating a new line of research that greatly expanded after his death.

One might ask why Clements himself did not play a more active role in the later development of these ideas. Certainly part of the

explanation lies in personality. Dogmatic and inflexible, he seemed psychologically incapable of acknowledging error or modifying his ideas. These personality traits were exacerbated by the political skirmishes that so dominated the later part of his career. Insecure in his embattled position, Clements was in no position to compromise with his critics. Another part of the answer was Clements's inability to assemble a dynamic research group. Successful research groups can be extremely effective in promoting the development of new lines of research. Using a suggestive analogy, David Hull claims that these groups are the intellectual equivalents of demes, the freely interbreeding populations of evolutionary biology.[69] The research group provides an informal social context within which ideas can be modified and transmitted more quickly than through the more formal channels of the extended scientific community. The group may also act as an efficient error eliminator. Nascent theories, even great ones, usually contain misconceptions, ambiguities, or unacknowledged assumptions. During the informal give-and-take between coworkers, ideas can be refined or modified before facing the scrutiny of outside scientists. Without the benefit of an effective research group a scientist may still be productive, but he is deprived of an important mechanism for perfecting, expanding, and perpetuating ideas. Such was the case with Clements. Many pieces of his theoretical system were useful, but he was unable to create a coherent intellectual tradition.