THE DEVELOPMENT OF PLANT ECOLOGY 1790-1960

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Declaration

This thesis has been composed by myself and the research on which it was based was my own work.

Abstract

The thesis charts the development of vegetation science from its beginnings. In the first chapter, particular attention is given to the work of Alexander von Humboldt and to the genesis of the idea that vegetation exists in natural units. A tradition of Humboldtian plant geography is traced to the end of the nineteenth century and the birth of self-conscious plant ecology. The second chapter follows the development of different notions of the plant association, and different forms of scientific practice, by F.E. Clements in Nebraska and J. Braun-Blanquet in Montpelier. Chapter Three describes the career of Henry Allan Gleason and follows the development of his individualistic concept of the plant association. Chapter Four examines the work of J.T. Curtis and R.H. Whittaker which revived the individualistic hypothesis and established it as dominant in the English-speaking world. The changing character of the scientific practice of plant ecology is correlated with interests, both internal and external to the discipline. A short coda indicates that debate over the nature of vegetation continues.

The thesis is narrative history, written throughout from a social and relativistic perspective.

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CONTENTS

CHAPTER TWO

Divergent Classifications - the Clementsian and Sigmatist Conceptions of the Plant Association

CHAPTER THREE

Henry Allan Gleason and the Individualistic Hypothesis

INTRODUCTION

In recent years the science of ecology has gained a fresh prominence. The knowledge of the natural world which ecology generates has become newly conspicuous in a wide cultural context, playing a prominent role in current debates as to the character of the natural world. Ecological knowledge is brought to bear on such problematic matters as the limits Nature sets upon Man's actions and the appropriate models for human behaviour.[1] Ecology today, one might maintain, has as central a role in the controversy over how Nature is best thought of as Darwinism had in the latter half of the nineteenth century. Yet the history of ecology, the development of its present character, has so far received little attention from historians and sociologists of science. No adequate histories of the discipline exist. In Donald Worster's vivid and suitably Western simile, ecology "is like a stranger who has just blown into town, a presence without a past."[2]

This scholarly neglect is to be deprecated. Even setting aside the cultural importance of ecology as a source of environmental imagery and rhetoric, ecology has become a large and important component of current scientific activity. The history and sociology of science is clearly incomplete without the history and sociology of ecology. However, there have been encouraging signs recently that scholars are beginning to rectify this unsatisfactory situation.[3] The present thesis is intended to aid that process.

I did not set out to provide a complete history of ecology. Ecology is a massive and multi-faceted subject and such a task would be beyond a single author, or at least beyond a single graduate student. My thesis is confined to the history of plant ecology and, even there, I have been very selective in order to bring the subject-matter into something like manageable proportions. I hope, however, that the thesis will be a worthwhile contribution to the history of ecology as a whole, since plant ecology is probably the oldest of the discipline's specialties, and is certainly one of the largest. While it is unwise to extrapolate from one branch to another of such a diverse subject, there is no doubt that the history of plant ecology exemplifies many of the problems, preoccupations and formative influences experienced by other ecological specialties.[4]

Scope of the historiography of ecology

The term 'ecology' is nowadays notoriously protean and multivocal. So I ought to make it clear at the outset that this thesis does not set out to provide a history of environmental thought or environmentalist political action. Rather it is primarily the history of a scientific specialty - or, more accurately, the history of a form of scientific practice. This is ecology as done by professional botanists, employed in universities or research institutions, who publish accounts of their work in scientific journals.[5] These people may or may not have any sympathy or connection with the concerns of Henry Thoreau or the activities of the Sierra Club. They are employed to generate knowledge about vegetation, either as an activity of pure academic research or to help supply society's material wants. If ecologists do these activities well, they may achieve the conventional rewards of a successful scientific career.

Academic ecology must be considered as, to some extent, an autonomous activity in the way that many of the disciplines of modern science are. It has its own subculture or subcultures, its own vested interests, its own prizes and professional rewards for its members to gain. It produces a distinctive form of scientific knowledge. Thus any adequate history of ecology must be 'internal' history in that it must contain a convincing account of the discipline's investigatory practice, its technical and cognitive developments, and its professional structure.[6] Any history of ecology which failed to take these elements seriously would miss the raison d'être of ecology as a scientific discipline.

However ecology, as well as having in some respects the character of an autonomous discipline, is also a dependent part of a much larger institution. It is a component of the scientific enterprise as a whole. The rewards which ecologists seek are often not entirely the property of ecology per se, but are offered within the larger professional frameworks of botany, zoology, or biology.

For instance, there are still relatively few professorial chairs in ecology. Most plant ecologists, if they are to be professors, must occupy chairs of botany or, at least, chairs within botany departments. The research funds available to ecologists would, generally speaking, be spent elsewhere in biological science, if they were not directed toward ecology. Research funding is usually awarded on a competitive basis. Similar competition surrounds the allocation of staff appointments between the various biological specialties. Thus the external relations of the specialty of ecology are often with other parts of the scientific community rather than with the wider society outside science. It is one of the principal themes of my thesis that the nature of the interface between ecology and the rest of science is of crucial historical importance.

Science is an exclusive and hierarchical institution.[7] Status and authority are not distributed equally throughout all its branches. It maintains its boundaries by employing criteria as to what is good and what is bad knowledge. Ecology has always been a discipline of comparatively low status. The welfare of scientific ecology has therefore been dependent upon the institutionalised judgements of ecologists' colleagues in other fields. This has led to problems for ecology.[8] Ecologists have frequently been faced with convincing other scientists of their discipline's scientific respectability for fear of being denied the full benefits that accrue to accredited members of the scientific community. The problematic nature of their status has been a formative influence on the behaviour of ecologists and the character of the discipline. Many of the attempts that have been made to reform the discipline's practice can only be understood as attempts to remove this difficulty. Thus the disciplinary history of ecology must take into account its position within the larger institution of science.

But I have also tried to show in the following chapters that the history of ecology, if it is to be true to its subject, can never be entirely self-contained disciplinary history, even in the extended sense of 'disciplinary' employed above. It must also connect with wider social, political and intellectual issues. It must be external history every bit as strongly as it is internal history. Indeed the history of ecology may be regarded as of great interest as a source of case-studies of the interaction between internal and external factors in the history of twentieth-century science. Or, perhaps more cogently, it might be regarded as providing excellent evidence of the artificiality of the internalist/ externalist dichotomy.[9] Every scientist does his work situated within a constellation of social interests, ranging from those of his sub-group of the profession, to those of the institution in which he is employed, those of scientists as a whole, those of his family, his local or regional community, and those of wider social or political groupings.

All these different sorts of social interests have equivalent status as bases for the explanation of actors' behaviour.[10] I have felt free to invoke one or another without restraint - using whichever appeared to me to have explanatory force in the given circumstances. On certain occasions, for example in my treatment of Henry Allan Gleason, my interpretations are based chiefly on the consideration of 'internalist' social factors. On other occasions, in particular in my treatment of F.E. Clements, I employ external social interests as the most important explanatory device. On still other occasions, for example in discussing Herbert Mason and Stanley Cain in Chapter Four, I point to the importance of the position of ecology within the larger institution of science. I believe no inconsistency is thereby created.[11] Such eclectism is required if the full complexity of the forces that shaped ecology is to be revealed.

That the history of scientific ecology is interwoven with social interests and intellectual trends of the most multifarious provenance ought not to surprise us. Ecologists study what one might call the face of Nature - the immediate and attractive features of the natural, as opposed to the man-made, world. They are thus occupied with a subject-matter which is the closest of all the scientific disciplines to what is referred to as 'Nature' in every-day usage and in the usage of the humanistic disciplines - 'Nature' as in Nature Study, the nature of woods, trees, flowers, streams, soil and rocks. One might say that ecologists study everything that interested Wordsworth save milkmaids and the shadows of clouds on the land. In the public imagination ecologists are Nature-Scientists in the way Wordsworth was a Nature-Poet.[12] But Man's relationship to Nature is not simply an aesthetic one. One needs only a little acquaintance with Wordsworthian moralising to understand this. Nor is it entirely a technical exercise in prediction and control, designed to supply mankind's material requirements, or construct a coherent conception of the world, although ecological inquiry clearly aids these enterprises.[13] The idea of Nature is a powerful one in other spheres. As Mary Douglas has pointed out, to argue that some action is "against Nature" is a powerful act of disapprobation.[14] Natural knowledge has an active role in society - or, rather, men and women actively use conceptions of the natural order to argue for particular social, moral and political ends.[15]

The view of Nature inherent in twentieth-century science may be secular in comparison with that of previous centuries, but the potential of the natural order as a moral resource is far from having been eliminated. Recent debates on the 'environmental crisis', or over the claims of sociobiology, show that the drawing of social and moral implications from what are regarded as the facts of nature is still a tenable polemic strategy. The subject-matter of ecology is such that the knowledge it creates is particularly amenable to use in this way. We may no longer be willing to see sermons or images of society in the physics of fluids, as seventeenth- or even nineteenth-century commentators were, nor in the subject-matters of geology or quantum physics, but we still see them in the 'Wordsworthian' natural world of ecological science.[16] I will argue that some of the most 'internal' technical features of scientific ecology bear witness to a willingness to argue from Nature as to what men ought to do, or what society ought to be.

Themes and structure

As mentioned above, this thesis is not meant to be a complete history, even of plant ecology. It has a much narrower compass. But its topic, although specific, is one that has been selected for the light its investigation sheds upon the historical character of the discipline as a whole. I intend in the following chapters, to elucidate the discipline's development by examining one of its most enduring preoccupations - a preoccupation that has often been the focus of controversy - the nature of the plant community. These controversies and the changing nature of this preoccupation embody and exemplify many of the cognitive and social interests which have existed within the discipline, and illustrate the effect of the external pressures exerted upon it.[17]

Even within this narrow compass, my treatment is not comprehensive or universal. The thesis is built around four selected case-studies. The first chapter investigates the origins of the scientific study of vegetation, paying particular attention to the work of Alexander von Humboldt. I draw upon the work of Michel Foucault to argue that the appearance of an interest in the phenomena of vegetation was a product of the emergence of a new cognitive order, in Foucault's terms a new episteme, in the later eighteenth century.[18] Furthermore, I propose an explanation as to why vegetation, when it first became an object of scientific study in its own right, was conceived of as existing in natural units - in definite plant communities. The belief that vegetation could be classified into natural units was to be a major tenet of ecological theory for many years. Its origins have, however, never previously been elucidated. Next, I describe the adoption of Humboldt's work on vegetation, firstly by botanists directly associated with him, and then more widely and by successive generations of workers. I will argue that the development of the Humboldtian legacy by these botanists founded a distinctive research tradition centered upon the study of the collective phenomena of plants. I believe that my first case-study sheds fresh light on the origins and early development of ecology and identifies important and hitherto unrecognised features of nineteenth-century biological science.

The second case-study takes as its subject the further development of the study of vegetation in two countries, the United States of America and France, in the early part of the twentieth century. A comparison is made between the ecological theory and practice of F.E. Clements and his associates and that of J. Braun-Blanquet and the Sigma school. I examine how differences in the social and institutional settings of plant science in each country led to divergent conceptions of the plant community and divergent classifications of vegetation. The comparative method was adopted in this chapter because the cultural and social nature of the activity of vegetational classification is thereby more clearly displayed - as is the contingent flexibility of the research tradition which was inherited from the Humboldtians.

The subject of the third case-study is the ecological career of Henry Allan Gleason - an American ecologist who was the originator of what became known as the individualistic hypothesis. This was a theory that vegetation did not occur in natural units and that the only real phenomena of vegetation were those of the individual plants. I construct the first full account of Gleason's career, interpreting Gleason's advocacy of an individualistic viewpoint in the light of his possessing professional commitments outside the mainstream of American ecology. Despite these outside commitments, and despite his individualistic conception of the plant community, Gleason's ecological work was still within the tradition of studying the collective phenomena of plants, the origin of which we see in the first case-study. His activity, like that of Clements and Braun-Blanquet, was genetically related to Humboldtian plant geography. Thus in the work of Gleason we see further exemplification of the potential for change and alteration, in response to new circumstances, possessed by a continuous tradition of research.

Gleason's theories survived intense early unpopularity and were eventually victorious, at least as far as ecology in America is concerned. The individualistic hypothesis, or something very like it, was re-assessed and revived in the nineteen-forties and -fifties. It came to dominate thinking on plant communities. The fourth case-study investigates this transformation of American plant ecology. The stresses which the discipline experienced in the nineteen-forties are examined as the background to the many calls for reform. The character of the complaints made against the status quo and the character of the innovative research initiated, are both considered in the light of pervasive and powerful culturally-given criteria as to what was good scientific knowledge. I examine the work of R.H. Whittaker in Tennessee and of J.T. Curtis and his associates in the University of Wisconsin. Both these workers offered fresh empirical and theoretical support for the individualistic hypothesis. The greater persuasive effectiveness of the Wisconsin work is interpreted in the light of J.T. Curtis's authority, experience and status within the scientific community.

With this fourth case-study, the thesis comes, in a sense, full circle. It has looked at the origin of research into natural units of vegetation; it has examined two of the twentieth-century schools which employed the idea of natural units in their practices; it has examined the genesis of an alternative conception of vegetation; and finally it examines what might be called the beginnings of the end of the idea that plants occur in natural groups. The four case-studies thus form a pattern which encapsulates much of the history of the discipline of plant ecology as a whole. They were chosen for this reason. The thesis ends with concluding remarks and a short coda indicating that any resolution of the debate over the nature of vegetation is more apparent than real. The controversy has flowed, unabated, into other areas of ecological discourse.

Narrative history - sociologically enlightened

My selection of subject-matter for the thesis may seem arbitrary and incomplete. Much important work bearing on the nature of the plant community, done in Europe, Britain, Australia, the Soviet Union, and the Tropics, is omitted or referred to only in passing.[19] But the structure of the thesis has one virtue. The mode by which the account moves from Europe to America, from the nineteenth to the twentieth century, exemplifies what sort of scholarly enterprise I have attempted. The following chapters, although they may appear to contain the history of an idea - the concept of the plant community - are not meant to be History of Ideas as that historical genre is generally understood. Ideas are not in themselves the subject-matter of this thesis.[20] Ecological knowledge is treated as being essentially social - as actively developed and modified by groups of people in response to practical contingencies.[21] I concentrate upon how both the cognitive and the practical aspects of a form of culture (using 'culture' in the anthropological sense) change as the practitioners find themselves in different circumstances or as cultural transfers are made from one country to another, and from one generation to the next.

It should be noted also that the phrase 'history of plant ecology' as used above to describe the subject-matter of the thesis, is also somewhat misleading. Continuity and identity can be no more safely assumed for disciplines than it can be for ideas.[22] I do not claim, for example, that those nineteenth-century European botanists who first studied the plant community were really doing 'ecology', before the word was coined. All that is claimed is that they, like the American ecologists of the twentieth century, looked at the collective phenomena of plants, and that their practices and achievements are, in some way, connected genetically with the practice of the later workers. Indeed the thesis is perhaps more a story of change and adaptation within scientific culture than it is an elucidation of the roots of ecology or its disciplinary history.

It will be obvious to some readers of the following chapters that my historiography is enlightened, if that is the right word, by my connection with and adherence to a particular school within the sociology of scientific knowledge - namely the practitioners of the 'strong programme' as set out in the work of Barry Barnes and David Bloor.[23] My approach is relativist. I have endeavoured not to be evaluative as to the truth-content of actors' beliefs. Belief is referred not solely to input from the natural world but primarily to the social circumstances which sustain it. Knowledge is regarded as the product of social construction and invention. The process of social construction of knowledge is held to be structured around the social and cognitive interests of the participants.

However, my principal intention in the writing of this thesis has not been to aid the study of the sociology of knowledge. I have felt myself to be writing not sociology, but history. Since history is a narrative form, my intention has been to present a narrative history of ecology - a tale of the doings of men and social groups in various places and times, and of the events and social interests with which they were confronted and in the light of which they framed their actions. If the narrative, as narrative, fails to suspend the reader's disbelief, nothing, certainly not sociological theory, can redeem it.[24]

This is not to say that reference will not be made in the following to the literature of the sociology of science. In our culture, at least, the plausibility of historical narrative is buttressed in different ways from that of, say, works of fiction or fairy stories. Historical narrative is routinely supported by explicit reference to evidence derived from sources, principally textual sources, which are independent of the narrative text itself. The plausibility of historical narrative is held to depend on such support. A historian must, however, work not only with textual evidence but with a view of man and of society. This, of necessity, underpins his explanations but is, unlike the evidential relation, more often than not implicit. The reader of a historical account must identify these underlying assumptions as best he can, often accepting or rejecting the history as he agrees or disagrees with the conception of human nature each particular author employs. In this thesis I have attempted on occasion to use the literature of the sociology of science to make explicit the conception of the nature of human activity which underlies the historiography. I hope the overall plausibility of my narrative is thereby increased.

I have also used the sociological literature in an illustrative manner. For instance, towards the end of Chapter One, I refer to the work of T.S. Kuhn and Barry Barnes on the nature of scientific discovery, and in particular to T.S. Kuhn's account of the discovery of oxygen. My purpose there is simply to help the reader to understand the genesis of the category 'plant association' by pointing out that the process underlying the recognition of this category was similar to that described by T.S. Kuhn for the origins of the category 'oxygen'. By referring to this literature, I am not making any statement about what the nature of the process of scientific discovery in general may be. My intention is simply to clarify for the reader, by illustrative examples, a particular discovery process.

It is in these instrumental modes that I use the sociological literature in the following narrative. Sociology of science has been unreservedly forced into service for the history. This usage is unashamedly eclectic, opportunistic and may be somewhat uneven. I have taken the liberty of making my constructions with whatever materials were available and seemed appropriate at the time.

Sociological generalisations have for the most part been eschewed. I hope, however, that sociologists of science will find my narrative interesting, and that they will find it useful for their own purposes. But, as mooted above, the final product must stand or fall as narrative - as an imaginative reconstruction of the past.[25]

A Motto for the thesis

The sophisticated and insightful papers of the late Robert H. Whittaker have been an indispensable aid to my understanding of ecological classification and the history of vegetation science more generally. My many specific debts to his work are acknowledged in the following pages, but my general indebtedness deserves special mention here. Because of his writings, my relativistic and culturally-orientated approach to the activity of ecological classification is not entirely novel. One of his many perceptive remarks on this subject might stand as the motto of my thesis:-

> "The basis of understanding and judging classifications cannot be one of literal verisimilitude or fidelity to nature. Rather than this, one finds that classifications develop in accordance with whole systems of interbalanced ... judgements ... A classification must be viewed as a cultural product, understood in a context which includes both cultural values and ecological conditions, and judged in its functional relation to present understanding and practice. Emphasis in this account of certain things - personal choice and judgement, intuition and subjectivity, cultural influence and precedent ... runs counter to what is usually sought in an account of scientific method ... The question here, however, is less one of ultimate objectives of science in general than what actually happens when natural communities are classified."[26]

CHAPTER ONE

ALEXANDER VON HUMBOLDT, HUMBOLDTIAN SCIENCE, AND THE ORIGINS OF THE STUDY OF THE PLANT COMMUNITY

Introduction

Vegetation has always provided an important part of Man's experience of the world. We may assume that, from the earliest times, a coherent and communicable classification of plant cover was an essential aid to successful hunting, food-gathering and the choosing of sites for agriculture and settlement. All the modern languages retain words which refer to features of the Earth's plant cover, words which label and identify aspects of the immensely complex and diverse living landscape of plants. It is instructive to note how much of our everyday terminology for landscape refers to vegetation rather than to underlying land-form. Such terms as moor, heath, meadow, forest, tiaga, steppe, maquis, chapparral and many more refer to familiar and apparently distinctive groups of plants, to types of vegetation.[1]

In modern times, the practical importance of vegetation is not diminished and the study of the earth's plant cover has become a scientific business. Disciplines such as plant ecology have generated an esoteric and technical body of knowledge about vegetation. In the present chapter I examine the beginning of this activity - the earliest academic investigations of vegetation. I examine the cultural background from which the scientific study of vegetation sprang. I will also seek to use the insights thus gained to answer two questions - why did the study of vegetation arise when it did; and what gave the study of vegetation the character it then had? In other words, the present chapter investigates why and how the regional types of vegetation first became an object of scientific interest.

It is remarkable that these questions have not been posed by any previous scholar for, as we shall see, it is by no means self-evident that vegetation ought to be an object of scientific study, nor that it exists in natural units.

This chapter consists of two parts. The first examines the work and cultural background of Alexander von Humboldt for an explanation of the genesis of the study of vegetation. The section sub-headed "Why a science of vegetation?" sums up and concludes this first part. The remainder of the chapter examines how Humboldt's exemplar was taken up by other workers, leading to a distinctive tradition of Humboldtian plant geography characterised by the study of vegetation units.

Vegetation or Flora

Within botany, the study of vegetation is distinguished from the study of floristics. The study of plant-cover is different from the study of the species of plants. The flora of a given region simply consists of all the different plant species which grow there. The student of floristics, therefore, is interested in identifying the kinds of plants which grow in his study area. He may map their respective distributions; he may make generalisations about the character of a region's flora as a whole; but the level of analysis on which his scientific practice is based is essentially the individual species. The student of vegetation, on the other hand, studies a collective phenomenon, produced by many species together. [The apparently distinctive types of vegetation listed in the first paragraph above correspond, somewhat loosely, to what ecologists call 'plant communities']. Grass may be a distinctive feature of prairies and a forest may be mostly oak-trees. But the occurrence of species of grass within any given area does not evidence the existence of a prairie, nor the presence of species of oak a deciduous forest. Such, in principle, is the difference between the subject-matter of floristics and vegetation science - for the ecological character of vegetation, not to mention its visual or aesthetic impression, is the product, not simply of the presence or absence of particular species, but of the relative abundances and the different growth forms of its constituent plants.[2]

Historically the study of floristics developed before the study of the collective phenomena of plants. In the middle of the eighteenth century, botanists concentrated their efforts on finding plants and classifying the specimens into species and the species into higher taxa.[3] The results of field collecting were summed up in species lists or catalogues of all the plants present in a given study area. It was a novel development when some botanists began to write of vegetation as being an object worthy of scientific investigation in its own right, and began to describe plant communities, their gross appearances and their species compositions. This new concern became an important part of botanical practice in the early decades of the nineteenth century. Alexander von Humboldt was probably the first explicitly to recommend to botanists the study of "gruppen geselliger pflanzen" and to suggest relationships between types of vegetation and environmental conditions.[4]

Of course this is not to say that the botanists who worked before Humboldt were unaware of vegetation. They frequently found it convenient to refer to vegetational features, employing laymen's terminology for this purpose. Such references were often quite specific. Linnaeus, for example, in his Philosophia Botanica (1751) distinguished twenty-five different plant habitats and gave the genera characteristic of each one.[5] He was often very perceptive in his remarks on the distribution of vegetation.[6] But all his observations on vegetation in this context were made as an adjunct to his concerns in plant collecting and systematics - that is to say they were secondary to his floristic activities. Reference to vegetational features allowed him to specify more accurately the species he was describing and where it was to be found.[7]

Eighteenth-century natural historians might also hypothesize about the role of plants and animals in the "Economy of Nature".[8] This teleological line of thought might lead to observations upon the inter-relations between individual species, or between populations of plants or animals such as Linnaeus's famous arguments that the growth of each species of plant was controlled by a specific herbivorous insect, the numbers of which were likewise controlled by the insectivorous birds, and so on.[9] Certain historians have argued that this form of reasoning carries within it an assumption as to the existence of a supra-individual natural category, analogous to our present-day concept of the ecosystem.[10] But these supra-individual categories, however they were conceived, were not themselves explicitly made the objects of scientific inquiry nor do they resemble the study objects of nineteenth-century vegetation science.[11]

In contrast, the plant geography of Humboldt and those botanists he inspired and influenced, was centrally concerned with vegetation, its character, distribution, relation to environmental parameters and such like, and not solely or primarily with the individual plants or species. As Humboldt wrote in his "Personal Narrative of Travels":-

> "I was passionately devoted to botany ... and I flattered myself that our investigations might add some new species to those which have been already described; but preferring the connection of facts which have been long observed, to the knowledge of insulated facts, although they were new, the discovery of an unknown genus seemed to me far less interesting than an observation on the geographical relations of the vegetable world, or the migration of the social plants, and the limit of the height which their different tribes attain on the flanks of the Cordilleras."[12]

While a strong taxonomic component was necessarily retained, it was with the elucidation of supra-specific matters of this nature that Humboldtian botany was primarily concerned. There was thus a striking difference between Humboldt's principal objectives and the principal objectives of the Linneans. Humboldtian plant geography was to be vegetational geography. Floristic plant geography, centered on the elucidation of the distribution of plant species, was to have a somewhat separate development throughout the nineteenth century.[13]

While this distinction can readily be over-stated - many, perhaps most, Humboldtian botanists (Grisebach and Schouw for instance) undertook both forms of research and the difference between a unit of flora and a unit of vegetation was sometimes blurred or unimportant in practice[14] - it is clear that, in the early nineteenth century, vegetation presented a novel object for scientific inquiry.[15] Around the study of this newly-distinguished object, a new botanical specialism was to grow.

One of the most interesting aspects of this cognitive re-organisation is that not only did vegetation become an object of inquiry _per se_, but it also came to be conceived of as existing in regional types or units. The assumption that there are natural kinds of vegetation was one of the key elements in the rationale of the new practice. It is here, therefore, that our search for the origins of the study of the plant community must begin.

Not putting the phenomena first

How did these shifts of interest come about? What made possible a new form of scientific practice based upon a new object for scientific inquiry? The remainder of this chapter will be devoted to seeking answers to these questions.

I should make it clear at the outset that my account of the early recognition of vegetation and vegetation units as objects for study is not meant to be the account of a discovery or discoveries. I believe it is not helpful to regard the history of the origin of vegetation units as an event or series of events in which investigators stumbled upon or somehow otherwise came newly to discern a class of natural objects which had existed in the real world all along and had previously been mysteriously neglected or inadvertently misunderstood. In this context the classic language of discovery is inappropriate.[16] To employ it would be to commit the form of historiographical error which Andrew Pickering has recently termed 'putting the phenomena first' - that is the assumption that phenomena have an existence independent of the process by which they are observed.[17] Furthermore, conventional discovery accounts too often depend on an unwarranted separation between theory and observation - the assumption that observational data are by themselves sufficient to force theoretical change.[18]

I will argue that the new objects of vegetation were called into being as the result of a change in scientific practice. Behind the recognition of vegetation units lay an altered set of intellectual concerns and an altered set of scientific practices. As we have seen, eighteenth-century natural historians were well aware of vegetation. But the problems they concerned themselves with did not require that vegetation itself be a level of inquiry.[19] Likewise they made no great effort to identify unitary entities within it. But new cognitive interests led to information from the natural world being re-organised and re-grouped - re-processed one might say. It was not that a previously unperceived object was realised to exist among and in some relation to the objects already long recognised. It was rather that new cognitive concerns produced a new world in which novel objects were discerned.[20]

As we shall see, ever more strongly exemplified as the chapters of this thesis progress, vegetation is such a thing that it can be conceived of in a multitude of ways - each empirically satisfactory and consensually agreeable.[21] In this respect at least, the jungle is neutral. The key to understanding the ways in which vegetation has been conceived lies, for the historian, not in the vegetation itself but in the way in which the vegetation has been investigated - and in the cognitive frameworks which have sustained the various investigatory practices.

It follows from the above that when I make statements to the effect that Linnaeus had no unit of vegetation, no tacit criticism of Linnaeus should be read. Likewise I do not mean to imply that Humboldt and his followers possessed extra-ordinary powers of insight when I state that they recognised such units. Such statements are entirely descriptive. I am not arguing that Humboldt succeeded where Linnaeus and the Linneans failed. Rather this chapter is an attempt to understand why Humboldt and the Humboldtians ordered the world in a different way from their predecessors. I shall trace the intellectual concerns which led to natural phenomena and natural inquiry both being re-organised in a novel manner. But in respect of the validity of belief, I shall try to be as neutral as the vegetation.[22]

A new regionality and a new episteme

One of the most interesting aspects of the developing study of vegetation is that the differences between Humboldt and Linnaeus mirror and exemplify more general changes in the character of Natural History, indeed in the whole of natural inquiry, as the eighteenth century passes into the nineteenth.[23] Eighteenth-century natural history was, as Foucault puts it, "the nomination of the visible" - and not just seeing and naming, but seeing and naming systematically.[24] To Linnaeus, successful naming entailed the fitting of all nature into a grand taxonomy.[25] The classification of phenomena was the end of natural history:-

> "The first step in wisdom is to know the things themselves; this notion consists in having a true idea of the object; objects are distinguished and known by classifying them methodically and giving them appropriate names. Therefore, classification and name-giving will be the foundation of our science."[26]

Thus only those aspects of nature that were clearly describable, and describable in visual terms, were legitimate objects of inquiry:-

> "He may call himself a naturalist (natural historian) who well distinguishes the parts of natural bodies by sight and describes and names all these rightly ... "[27]

The paradigm example of an investigable object was, of course, the plant species as characterised in terms of certain obvious features of type specimens.

But nominating the visible was not to retain its dominant influence over the activity of natural historians throughout the entire century. Foucault has argued that the nineteenth century is separated from the eighteenth by a most fundamental transformation of culture and discourse. Beginning in the late half of the eighteenth century, a profound change took place in the totality of assumptions upon which knowledge of the actual world was based.[28] One aspect of this change was that scholarly emphases moved from the external features of objects to features and processes, integral but internal and unseen. We can see a shift from these preoccupations in, for instance, the work of Immanuel Kant, who has been identified by Foucault as a crucial harbinger of the new episteme.[29]

Of particular interest to our present discussion are Kant's lectures on "Physische Geographie".[30] To Kant, the systematic arrangement of things into taxonomies, according to selected visible features, as done by Linnaeus, was merely the aggregation of arbitrary and artificial divisions of nature.[31] Such an activity lacked:-

> " ... the idea of a whole out of which the manifold character of things is being derived ... In the existing so-called system of this type, the objects are merely put beside each other and ordered in sequence one after the other."[32]

For Kant, the essential prerequisite to a knowledge of the world was not an apparatus of logical classification working with isolated and recombined phenomena, but description of phenomena as they actually occur and co-exist in the world.[33] Physical geography could give "an idea of the whole in terms of area".[34] It was only after the preliminary task of geographical description had been undertaken that a proper "system of nature", based on real phenomena rather than arbitrary divisions and aggregations, would be possible.

German geographers, following Kant, assumed the existence of a functional interrelation between all of the individual features of the Earth's surface. In other words, they assumed an underlying causal unity of Nature, of which the visible forms of things were only one aspect. This unity of nature was, of course, quite universal. The earth was one whole. In 1811, the geographer Butte wrote "no scientist doubts the reality of an earth organism".[35] But the Earth was also regionalised in two important ways. One form of regionality was what Hartshorne has termed 'vertical unity', the interrelation between all the phenomena of any particular place or area.[36] Phenomena peculiar to a particular region were the cause of other equally regional phenomena - for example, climatic and environmental conditions affected the moral properties of men so that, as Kant wrote, "in the mountains, men are actively and continuously bold lovers of freedom and their homeland".[37] Another form of regionality was what Hartshorne has termed 'horizontal unity' - the unity of a region as an entity distinct from other neighbouring units.[38] Thus, although nature was conceived of as being a single holistic interrelated organism, there existed, within that large whole, other holistic structures which by reason of their internal interrelatedness had distinctive characters, and were distinguishable one from another. Nature was made up of distinct natural units.[39] As Macpherson puts it:-

> "Regional emphasis, the study of earth spaces, ... was one of the traditions in the organisation of German geography."[40]

Nor were such ideas confined to geographers. As Janet Browne has recently shown, use of the notion of regionality had also, by this time, appeared in the work of the late eighteenth-century practitioners of Linnean botany. Prior to 1760 or so, to write a Flora was simply to produce a list of plants, collected from an area arbitrarily or haphazardly delimited. But from that date onward, the concept was gradually formulated that flora and fauna were regionally differentiated.[41] The surface of the globe was held to be divided into natural regions and each region possessed a grouping of plants and animals with general characteristics peculiar to itself. The plants of Sweden, for instance, possessed the characteristics of a northern European botanical region, a Northern European 'nation of plants'.[42] And these characteristics were different from those possessed by the plants of Italy or Australia. The writing of Floras came thus to incorporate a chorological component. As Browne puts it, "the idea of biological provinces had begun to capture the imagination".[43] Floristic botany paralleled developments in geography; botany became itself geographical.

One of the earliest writers in whom botanical description has a strong geographical and regional structure was Johann Reinhold Forster. As the official naturalist, Forster sailed around the world with Captain Cook on Cook's second voyage (1772-1775).[44] Forster's account of his trip Observations made on a Voyage around the World, published in 1778, contains much geographical and botanical description. This was structured around a strong conception of regionality. Forster's regionality, like Kant's, was supported by a theory of environmental influence. Different skies, different climates, different prevailing winds were held to produce diverse sorts of vegetation and diverse forms of human society. He wrote of the Society Islands:-

> "The mild and temperate climate, under the powerful, benevolent and congenial influence of the sun, mitigated by alternate sea and land-breezes quickens the growth of vegetation; and therefore in some measure also, benefits and improves the human frame, by this happy combustion,"[45]

and, more generally, of the tropical islands:-

> " ... the climate softens what is savage in human nature, and I may say naturally leads to the civilisation of Mankind, the people are fond of variety of food, of conveniences at home and of neatness and ornament in dress."[46]

Forster's regions were not precisely delimited - they were held to grade into one another over broad areas of transition.[47] But the fact that the globe did not have a uniform climate necessarily entailed, for Forster, spatial differentiation of the natural phenomena of the Earth's surface. His principal explanation for such differentiation was the unequal application of the heat of the sun over the globe.[48] But it is important to note that the patterns of plant distribution he described were not solely latitudinal zonations as such an explanatory device might be held to entail. Forster observed that the flora of America was different, in important respects, from that of Asia even along the same band of latitude.[49] He held environmental factors such as heat or indeed overall climate to be of great importance:-

> " ... a similarity of situation and climate sometimes produces a similarity of vegetation, and this is the reason why the cold mountains of Tierra del Fuego produce several plants, which in Europe are the inhabitants of Lapland, the Pyrenees and the Alps".[50]

But similar environments did not produce wholly identical natural productions. The individuality and integrity of the 'nations of plants', like those of the nations of men, were explicable only if matters of origin and historical development were taken into account.[51] Like much contemporary German scholarship, botany became historical as well as geographical.

Forster's Observations contain much pleasant description of vegetation. The varieties of plants and of vegetation afforded an invaluable key to the understanding of the effects of the environment, and therefore to the general character of nature in any given region. Also the vegetation was one of the aspects of the environment which impinged most directly upon humanity. As Janet Browne points out, by insisting that plants mediated between the physical and the human sphere, Forster claimed botanical geography to be a subject of crucial and hitherto unrecognised importance.[52]

The importance Forster granted vegetation and the new significance of botanical geography are both evidence of how far cognitive concerns had altered since Linnaeus's time. Forster, while to a certain extent involved in taxonomy, was far from being primarily a nominator of the visible. But although his work exhibited a new awareness of vegetation as an interesting object in its own right and had a clear concept of regionality, his regions were at least primarily floristic units and not vegetational ones. Floristic analysis was how they were in practice recognised and differentiated:-

> "As the South-Sea is bounded on one side by America and on the other by Asia, the plants which grow in its isles, partly resemble those of the two continents; and the nearer they are either to the one or the other the more the vegetation partakes of it. Thus the easternmost isles contain a greater number of American than of Indian plants, and again as we advance farther on to West, the resemblance with India becomes more strongly discernible."[53]

Forster shows the new concern for vegetation and for regionality. His 'biological provinces' are indeed novel objects for scientific inquiry.[54] But they are not yet that novel object whose origins we are at present seeking. They are not vegetation units *per se*. The same can also be said of the concept of biological regionality to be found in the writings of Karl Ludwig Willdenow.

Karl Ludwig Willdenow: floristic plant geographer

Professor of Natural History and Botany at the University of Berlin from 1801 until his early death in 1817, Willdenow was indisputably one of the leading German botanists of the early years of the nineteenth century.[55] His major textbook *Grundriss der Krauterkunde* sold widely and influenced much later botanical work in Germany and beyond.[56] The *Grundriss* was first and foremost a textbook of taxonomic botany - it was intended to replace Linnaeus's *Philosophia Botanica*.[57]

Stress on nomination of the visible was still very prominent. A long section on terminology - one hundred and thirty seven pages in the second (1811) English edition, approximately one third of the book[58] - provided a detailed vocabulary for describing the external features of plants:-

> "The true knowledge of plants consists in the art of arranging, distinguishing and naming them ... "[59]

The visible structure of plants was proposed to be the principal object of botanical study:-

> "The first object of a student of Botany, after becoming acquainted with the terminology is to gain an accurate knowledge of every plant as it comes his way. He must acquire what may be called a botanical glance; that is he must accustom his eye to run over the stem, the leaves in all their structure, the mode of inflorescence, and all the other conspicuous parts of a plant, so as to discover by mere inspection, determinate characters distinguishing it from similar plants. In this way he becomes enabled to know plants by their external appearance ... With this knowledge, however, he must not be contented, but must examine more accurately the parts of the flower and fruit and be able to find in them certain and fixed characters ... "[60]

The study of the external features of plants was not abandoned in the context of the new episteme. It provided the basis for the development of taxonomic botany throughout the nineteenth and into the twentieth century. But nineteenth-century study of visible structure was by no means identical to that practised by the Linneans. Willdenow was, for example, concerned much more than Linnaeus ever had been with developing a natural system of classification - which would reflect the underlying similarities between species - to replace the artificial sexual system.[61]

The study of the visible structure was continued within a new cognitive framework, within which other phenomena were also important objects of study. Taxonomy was no longer the whole of botany. Willdenow's work expressed these new concerns - he was interested in the historical development of flora and of vegetation, and, like Forster, he conceived of the world's plant cover in terms of natural organic regions. [Willdenow had studied natural history under Johann Forster while a student at Halle in the late 1780s. He later acknowledged the large intellectual debt he owed Forster].[62]

The Grundriss contains a long section setting out what Willdenow termed the 'History of Plants' [Geschichte der Pflanzen] which he defined as:-

> " ... a comprehensive view of the influence of climate upon vegetation, of the changes which plants most probably have suffered during the various revolutions this earth has undergone, of their

> dissemination over the globe, of their migrations, and lastly of the manner in which nature has provided for their preservation."[63]

The characteristics of the world's plant cover were presented as interpretable in terms of historical processes - as being part of the history of the earth itself:-

> "When in this way, perhaps after a long succession of years ... the land was gradually formed, hurricanes, earthquakes and volcanoes might again destroy large tracts, and change the form of the land, by which means a number of plants might be destroyed that afterwards might never appear again ... Countries that are now separated by the ocean might formerly have been joined, at least the plants they have in common authorise the supposition. In this way might the most northern part of America have been connected with Europe and New Holland and the Cape of Good Hope."[64]

As we shall see in more detail shortly, the historical investigation of the earth as a whole was itself a novel element of the new episteme.

Willdenow's "History of Plants" contained much fine observation of vegetation. There was, for instance, a long and excellent account of the form of vegetational change which was later to be termed 'plant succession' - the process whereby the activities of the first species to colonise a particular site lead, by the accumulation of organic matter and the breaking down of the underlying rock, to the site becoming suitable for colonisation by other species:-

> "The decay of these mosses and smaller plants produces, by degrees, a thin stratum of earth, which increases with years, and now even allows some shrubs and trees to grow in it, till finally, after a long series of years, where once barren rocks stood, large forests with their magnificent branches delight the wanderers' eye. Thus nature proceeds, acting by degrees, always great, constant and intent on the good of the whole."[65]

He also described the corresponding process of succession which begins not with bare rock but with open water.[66]

But Willdenow did not investigate vegetation for its own sake. His remarks on vegetational development and other vegetational matters, while certainly those of a shrewd observer and a knowledgeable botanist, were incidental to his floristic concerns. His observations on vegetation were not central to his investigative enterprise. Willdenow's "History of Plants" was essentially a floristic form of inquiry - albeit different in many fundamentals from that of Linnaeus. It represents one of the first programmes for a separate botanical specialism to deal with plant distribution in relation to climatic, geographical, geological, migrational and other factors - what we might call self-consciously distinct plant geography.[67] But it was a floristic, not vegetational plant geography. It was based on the study of the distribution of the species of plants:-

> "Hence Canada produces different plants from Pennsylvania, this again from Virginia, this again different plants from Carolina and Carolina from Florida etc. Hence the northwest coast of North America produces plants which totally differ from those of the northeast coast, the southwest coast different plants from those of the southeast." [68]

Willdenow was here referring to the species of plants, not their forms of growth nor the general aspect of the vegetation.

Willdenow's plant geography had, like Forster's, and most contemporary German forms of geographical inquiry, a strong interest in regional divisions. But, again like Forster's, it did not contain the vegetational units the conceptual origins of which this essay seeks - for Willdenow's regions were floristic ones. He distinguished "five principal floras in Europe, to wit, the Northern Flora, the Helvetic, the Austrian, the Pyrenean, and the Appenninian Flora".[69] The distinctive character of each regional flora was to be established by the listing of the plant species present within it. This was Willdenow's principal geographical research project.

Willdenow's work is interestingly different from that of his predecessors. With its emphases on regionality and historical development, it displays the transformation which had overtaken botanical inquiry. It was of great importance in the development of floristic plant geography - it represents floristic botany becoming geographical. It shows, too, the beginnings of an interest in vegetation. But Willdenow's work, like Forster's, does not yet contain the approach to vegetation whose origins we are at present seeking.

Alexander von Humboldt and the new episteme

Alexander von Humboldt, however, never listed plants in the manner advocated by Willdenow. He and Willdenow, who was only five years his senior, shared a long and co-operative friendship, dating from 1788.[70] They had many scientific interests in common. Willdenow had done much to stimulate Humboldt's early interest in botany - particularly in the problems of plant distribution.[71] Willdenow owed something of his grasp of the floristic diversity of Europe to having examined specimens collected by Humboldt in his travels, in particular to the Iberian peninsula.[72] But Humboldt's botanical geography is, in some respects, as distinctively different in emphasis from Willdenow's floristics as Willdenow's was from Linnaeus's.

Alexander von Humboldt was a remarkable man of polymathic learning and a synthetic habit of thought.[73] He sought always to write what he termed 'physique générale' - the universal science which would speak of the unity of nature and which ought to be the chief end of all natural inquiry.[74] There was no one better qualified to take up that eclectic and harmonising task. But cosmological and holistic though his concerns always were, the geography of plants had an extremely important place within his grand scheme. It was one of the major routes toward the 'physique générale'.[75]

Humboldt formulated the outline of his programme for the study of the geography of plants as early as 1790, in which year he received important criticism and encouragement from George Forster, Johann Reinhold's son.[76] His ideas for the new science were first publicly set out in the Flora Fribergensis Specimen, published in 1793, when he was twenty-six:-

> "Observation of individual parts of trees or grass is by no means to be considered plant geography; rather plant geography traces the connections and relations by which all plants are bound together among themselves, designates in what lands they are found, in what atmospheric conditions they live, and tells of the destruction of rocks and stones by what primitive forms of the most powerful algae by what roots of trees, and describes the surface of the earth in which humus is prepared."[77]

Plant geography was thus, for Humboldt, the study of the collective phenomena of plants and the empirical investigation of why particular groups of plants flourish where they do. Unlike the old natural history, unlike Willdenow's floristic plant geography, it was not primarily the study of individual plants or species. Interested in taxonomic botany as he was, Humboldt had moved firmly away from the herbarium. He claimed to focus not upon arbitrary divisions of nature but upon real phenomena - and to be concerned not only with visible features but also with the investigation of underlying "connections and relations".[78]

Humboldt's emphases for his plant geography may thus be seen as congruent in character with changes taking place in many fields of natural inquiry - not only in geography and not only in Germany - as the eighteenth century faded. The older overweening pre-occupation with the visible was generally being abandoned as irrelevant in the face of a new desire to study the underlying organic cohesiveness of nature and the hidden, but nevertheless investigable, relationships between phenomena within it. The natural system of Antoine-Laurent de Jussieu superseded the Linnean sexual system; Lamarck succeeded Buffon; Treviranus coined a new name for a new scientific practice. L'Histoire Naturelle became la biologie.[79]

It is interesting that Abraham Gottlob Werner, under whom Humboldt studied at the Freiberg School of Mines, has recently been identified as a figure of major importance in the genesis of the new episteme.[80] Werner was the first to conceive of the possibility of a historical geology (geognosy). His new science transformed classical mineralogy - the study of individual mineral forms - and made possible the historical investigation of the earth as a whole. Werner's geognosy, like the new studies in comparative anatomy, involved:-

> " ... assembling, analyzing, relating and comparing a large number of distant facts which do not have the slightest apparent relation to one another."[81]

Albury and Oldroyd identify Humboldt as one of the first to adopt "Wernerian geognosy as a basis for world-wide research into the earth's history".[82]

I will attempt to show that as well as extending the Wernerian programme in geological science, Humboldt exmployed the framework of the new episteme to create a new science of vegetation. Humboldt made explicit the link between his attitude to vegetation and the new historical study of the earth:-

> "Geognosy (Erdkunde) studies animate and inanimate nature ... both organic and inorganic bodies. It is divided into three parts: solid rock geography, which Werner had industriously studied; zoological geography, whose foundations have been laid by Zimmerman; and the geography of plants, which our colleagues have left untouched ... This is what distinguishes geography from nature study, falsely called nature history; zoology (zoognosia), botany (phytognosia) and geology (oryctognosia) all form part of the study of nature, but they study only the forms, anatomy, processes, etc., of individual animals, plants, metallic things or fossils. Earth history, more closely affiliated with geography than with nature study, but as yet not attempted by any, studies the kinds of plants and animals that inhabited the primeval earth, their migrations and disappearance of most of them, the genesis of mountains, valleys, rock formations and ore veins ... the earth surface gradually covered with humus and plants ... "[83]

Thus Foucault's analysis, originally applied only to comparative anatomy and physiology as far as biological science was concerned, also offers important fresh insights into the history of Man's attitudes towards his natural environment. The emphasis of natural discourse changed. The new concerns with integrative processes, with invisible connections, with natural wholes, ushered in the study of new objects. Vegetation was one of these new objects. What had previously been simply the natural setting for the objects of taxonomic inquiry became a locus of study in its own right. Furthermore, vegetation and Man's relation to it came to be conceived of in holistic integrative modes.

The cognitive concerns of the new episteme were distributed quite generally throughout European natural science. We have seen some of them also in the writings of Johann Reinhold Forster and Karl Willdenow. But one might say that they were particularly strongly institutionalised in the University of Göttingen, where Blumenbach, Zimmerman and Treviranus taught and where Humboldt had been a student, and in various French institutions such as the

Muséum d'Histoire Naturelle in Paris, with whose faculty Humboldt developed strong links during his long residence in Paris after 1804.[84] When, in 1807, Humboldt further articulated his idea of a plant geography in his Essai sur la Géographie des Plantes, the French edition was dedicated to Antoine-Laurent de Jussieu and René Desfontaine, both professors at the Muséum d'Histoire Naturelle.[85] The Essai clearly bore the marks of the new episteme.

Contributions to the literature of scientific travelling

The first draft of the Essai had been composed on the lower slopes of Chimborazo in 1802, during Humboldt's travels in South America. This provides another important clue as to the cultural background from which the Essai sprang. Humboldt saw the making of scientific journeys as an essential part of the method of natural inquiry. Travel was obligatory for any scholar who sought to grasp both the diversity of phenomena and the essential unity of nature. Humboldt had been introduced to the art of scientific travelling by an experienced practitioner, the younger Forster, with whom he travelled in Germany, Flanders, Holland, France and England in 1790.[86] George Forster had been round the world with his father, Johann Reinhold, on Captain Cook's second voyage, and had very successfully published an account of their travels.[87] After his journey with Forster, Humboldt was continually making plans to undertake an important scientific expedition of his own.[88] The journey to the Americas was the culmination of a long programme of preparation and training. There is no doubt that it was also a turning point in his life. It has a crucial place within any account of his intellectual concerns and interests.

The expedition to the Americas - with Aimé Bonpland as companion - lasted five years but Humboldt spent many more years collating and publishing its results. Although he also made a long journey to northern and central Asia,[89] the fact that in the New World he had visited the tropical zone, where plant and animal life were developed to their greatest richness and the natural productions were exotically different from those of Europe, meant that the journey to the Western Hemisphere was always the more important of his two major scientific expeditions.[90] The expense of the American journey and its aftermath - compiling and publishing its results - swallowed up most of his private fortune.[91] It was a project to which he was deeply committed, and more than merely intellectually.

Writing about one's travels was already a well-accepted form of scholarly activity before Humboldt. Here too Humboldt learned from George Forster. Shortly after their return to Germany in 1790, Forster published a description of the journey he and Humboldt had made.[92] Ansichten vom Niederrhein was acclaimed in literary circles, particularly by Goethe, Schiller and Alexander's brother, Wilhelm von Humboldt.[93] From a comparison of Forster's and Humboldt's travel writing,we can see that they were both active within the same genre. There is much of Forster's model in Humboldt's several accounts of his own travels in South America.[94] Both men paid particular attention to the morphology of landscape. Both favoured panoramic description. Both sought scientific accuracy and collected all manner of detail and data. Both combined these scientific concerns with avid recording of subjective impression. Such harmonisation of science and subjectivism was seen, by the literary men contemporary with Forster and Humboldt, as new, exciting and a sign of a fresh maturation of natural inquiry.

It is, thus, a measure of the importance of plant geography in Humboldt's eyes that the Essai was planned as the introductory volume to the full scientific account of his expedition.[95] It was, to Humboldt, the piece of work which encapsulated, scientifically and aesthetically, the totality of the impression made upon him by the tropics of South America:-

> "Mais j'ai pensé qu'avant de parler de moi-même et des obstacles que j'ai eu à vaincre dans le cours de mes opérations, il vaudroit mieux fixer les regards des physiciens sur les grands phénomènes que la nature présente dans les régions qui j'ai parcourues. C'est leur ensemble que j'ai considéré dans cet essai. Il offre le résultat des observations qui se trouvent développées en détail en d'autres ouvrages que je prépare pour le public.
>
> J'y embrasse tous les phénomènes de physique que l'on observe tant à surface du globe que dans l'atmosphère qui l'entoure."[96]

The holistic unity of landscape

The patterns of plant distribution were a key to underlying regularities within the natural world:-

> " ... as the human race in its development must pass through certain stages of civilisation, so also is the gradual distribution of plants dependent on definite physical laws."[97]

But these regularities in nature could only be understood holistically and not reductively, for nature was one holistic unity:-

> "Cette science, qui constitue sans doute une des parties le plus belles des connaissances humaines, ne peut faire de progrès que par l'étude individuelle, et la réunion de tout les phénomènes et de toutes les productions que présente la surface du globe. Dans ce grand enchaînement de causes et d'effets, aucun fait ne peut être considéré isolément. L'équilibre général qui règne au milieu de ces perturbations et de ce trouble apparent, est le résultant d'une infinité de forces mécaniques et d'attractions chimiques qui se balancent les une par les autres; et si chaque série de faits doit être envisagées separement pour y reconnoître une loi particulière, l'étude de la nature, qui est le grande problem de la physique générale exige la réunion de touts les connaissances qui traitent des modifications de la matière."[98]

Furthermore, and it was a topic possibly more important even than the above, Humboldt argued that vegetation mediated between the natural world and human society. Thus botanical geography had the same central importance to Humboldt that it had to Johann Forster. With a form of argument similar to contemporary Neo-classical theories of painting, Forster had stressed the unities within landscape, unities in which Man participates, partly due to the moral influence of vegetation.[99] Humboldt developed further, within his own plant geography, Forster's view of the effect of the natural environment on Man. To Humboldt, the vegetation was both an expression of the physical environment and an important part of the environment as it affected the races of Man, materially and spiritually. the passage with which Humboldt introduced this subject is important enough to quote at length:-

> " ... mais l'homme sensible aux beautés de la nature y trouve encore l'explication de l'influence qu'exerce l'aspect de la végétation sur le gout et l'imagination

des peuples. Il se plaira à examiner en quoi consiste ce que l'on nomme le caractère de la végétation, et la variété de sensations qu'elle produit dans l'ame de celui qui la contemple. Ces considérations sont d'autant plus importantes qu'elles touchent de près aux moyen par lesquels les arts d'imitation et la poésie descriptive parviennent à agir sur nous. Le simple aspect de la nature, la vue des champs et des bois, causent une jouissance qui diffère essentiellement de l'impression que fait l'étude particulière de la structure d'un être organisé. Ici, c'est le détail qui nous intéresse et qui excite notre curiosité; là, c'est l'ensemble, ce sont des masses, qui agitent notre imagination. Quelle impression différente cause l'aspect d'une vaste prairie bordée de quelques groups d'arbres, et l'aspect d'un bois touffu et sombre mêlé de chênes et de sapins? Quel contraste frappant entre les forêts des zones tempérées, et celles de l'équateur, où les troncs nus et élancés des palmiers s'élévent au-dessus des acajous fleuris, et présentent dans l'air de majesteux portiques? Quelle est la cause morale de ces sensations? sont-elles produites par la nature, par la grandeur des masses, le contour des formes, ou le port des végétaux. Comment ce port, cette vue d'une nature plus ou moins riche, plus ou moins riante, influent-ils sur les moeurs et surtout sur la sensibilité des peuples?"[100]

Thus, the regional distribution of kinds of vegetation correlates with and is, to some extent, a cause of, differences in aesthetic sensibility and moral development between races and cultures. Note here that it is the vegetation <u>en masse</u> that is active in this respect. It is the complete impression presented by the vegetation as a whole which leaves the vital imprint on the mind of "l'homme sensible":-

"The poetical works of the Greeks and the ruder songs of the primitive northern races owe much of their peculiar character to the forms of plants and animals, to the mountain-valleys in which their poets dwell, and to the air which surrounded them ... However much the character of different regions of the earth may depend upon a combination of all these external phenomena, and however much the total impression may be influenced by the outline of mountains and hills, the physiognomy of plants and animals, the azure of the sky, the form of the clouds and the transparency of the atmosphere, still it cannot be denied that it is the vegetable covering of the earth's surface which chiefly conduces to the effect."[101]

The individual plants are involved only as they contribute to this larger whole.

This holistic emphasis on vegetation rather than individual plants ran throughout Humboldt's treatment of plant geography, not only in the Essai but also in his later works. It forms, as we have seen, one of the principal reasons why his work may be distinguished from that of the Linneans and even from that of Willdenow. Humboldt acknowledged the importance of the study of individual plants and their species. But this was not the principal focus of his interest:-

> "Les recherches des botanistes sont généralement dirigées vers des objets qui n'embrassent qu'une très-petite partie de leur science. Ils s'occupent presque exclusivement de la découverte de nouvelles espèces de plantes, de l'étude de leur structure extérieure, des caractères qui les distinguent, et des analogies qui les unissent en classes et en familles.
>
> Cette connaissance des formes sans lesquelles se présentent les êtres organisés, est sans doute la base principale de l'histoire naturelle descriptive ... mais si elle est digne d'occuper exclusivement un grand nombre de botanistes, si même elle est susceptible d'être envisagée sous des points de vue philosophiques, il n'est pas moins important de fixer la Géographie de plantes; science dont il n'existe encore que le nom, et qui cependant fair une partie essentielle de la physique générale."[102]

Humboldt's concern with holistic structures and the unity of landscape is well-exemplified by the "Tableau Physique des Andes et Pays voisins". This is a large and elaborate engraving of a cross-sectional profile of the Andes from the Atlantic to the Pacific at the latitude of Chimborazo. It is folded within the pages of the Essai.[103] In the one illustration were mapped or tabulated:- where plant species grow, where the altitudinal zones of vegetation begin and end, which animal species live where, the forms of agriculture pursued, the underlying geological structures, and all manner of measurable physical parameters. The object was to give, at a single glance one might say, a complete impression of a natural region - the "régions équinoctiales" of South America.

Humboldt's Romanticism and Naturphilosophie

The "Tableau", with its holistic vision of a unified landscape, did not merely represent a conception unique to Humboldt but rather one which sprang from the wider background of German Romanticism and Naturphilosophie. Humboldt had a close intellectual association, albeit a brief one, with Schiller;[104] he wrote an essay, "The Genius of Rhodes", which was an allegory upon the principle of life conceived of as chemical affinity, for Schiller's influential periodical Die Horen.[105] Humboldt also had a much more enduringly sympathetic association with Goethe.[106] The German edition of the Essai sur la Géographie des Plantes, entitled Ideen zu eine Geographie der Pflanzen, was dedicated to Goethe.[107] The dedication page was illustrated with an engraving which represented the genius of Poetry unveiling Nature. In the foreground lies an open copy of Goethe's great botanical work Die Metamorphose der Pflanzen.[108] Goethe enthusiastically studied Humboldt's work on plant geography and drew an illustration for the text, "a conventional picture" of "a symbolic landscape", which he in turn dedicated to Humboldt.[109]

Although Humboldt was later to be vehemently criticised by Schiller,[110] and to have serious scientific disagreements with Goethe, he never repudiated his early connections with the leaders of the German Romantic movement.[111] He reprinted his allegorical essay "The Genius of Rhodes", ten years after its original publication, in his "favourite" and most "purely German" work, the compilation volume Ansichten der Natur.[112] Humboldt's last and most ambitious major work, Die Kosmos, written almost forty years later still, contains many passages which give high praise to the Naturphilosophen.[113] Goethe's influence is acknowledged in the book's introduction and much of the text is redolent of the Romantic tradition, continuing to evince intellectual concerns seen in Humboldt's earlier works - in the Essai and, especially in Ansichten der Natur.[114]

His contact with Romanticism is perhaps most obvious in the importance Humboldt attaches to aesthetics within natural inquiry. In Humboldt's view, an author writing about Nature must self-consciously aim at creating a work of art and not merely give an accurate account of scientific research:-

> "With the simplest statements of scientific facts there must ever mingle a certain eloquence. Nature herself is sublimely eloquent. The stars as they sparkle in the firmament fill us with delight and ecstasy, and yet they all move in orbit marked out with mathematical precision."[115]

Man's attitude to natural phenomena must thus combine aesthetic appreciation with rigorous scientific procedure. It was not that the scientific faculty comprehends while the aesthetic faculty merely appreciates. The aesthetic component is not passive in the comprehension of nature. For example, aesthetic reactions to different sorts of vegetation are evidence as to the nature of the effects of the natural environment upon Man and upon culture. Our aesthetic responses to natural phenomena count as data about these phenomena. They are also guides and sign-posts for our scientific investigations. And, even more importantly, Science, if it is to be true to Nature, must ultimately be aesthetically satisfactory.

Important recent studies into German Naturphilosophie have shown that attitudes as to the role of aesthetics often provide crucial clues as to important distinctions to be made with Naturphilosophie as a whole.[116] A major problem facing the philosophy of natural inquiry at the end of the eighteenth century was how human reason, which had only sense data to work with and was thus confined to the scrutiny of external characteristics, could ever come to comprehend the inner realities of things. The Kantian response was to argue that reason simply could not have direct access beyond the phenomena. The best one could hope for was, through establishing systematic interconnections and law-like relationships, to relate natural phenomena into a synthetic holistic scheme. But that variety of Naturphilosophen which von Engelhart has termed 'romantic' or 'speculative' were not prepared to accept a necessary dichotomy between the understanding of the investigator and the object being investigated. They proposed an alternative solution by which a theory of aesthetics came to the aid of the theory of rationality. Man's aesthetic sensitivities could, if suitably trained and applied, transcend the limitations of reason, penetrate beyond the surface phenomena and, sensuously and intuitively, grasp the underlying unities of Nature.

Humboldt is clearly, to some extent, sympathetic to this point of view:-

> "[W]ho is there that does not feel himself differently affected beneath the embowering shade of the beeches grove, or on hills crowned with a few scattered pines, or in the flowering meadow where the breeze murmur

> through the trembling foliage of the birch? A feeling of melancholy, or solemnity, or of light buoyant animation is in turn awakened by the contemplation of our native trees. This influence of the physical on the moral world - this mysterious reaction of the sensuous on the ideal, gives to the study of nature, when considered from a higher point of view, a peculiar charm which has not hitherto been sufficiently recognised."[117]

Such sentiments are to be found throughout Humboldt's entire corpus. The degree to which plant geography involved aesthetic judgement and shared its subject-matter with landscape painting was, for Humboldt, one of its great attractions and sources of significance.[118]

Commitment to empirical science

But Humboldt, although always alive to the prerogatives of aesthetic sensitivity and the appeal of the Sublime, does not follow Schiller or Schelling in denigrating the fruits of rationality. He was chastised by Schiller for his "keen cold reason which would have all nature shamelessly exposed to scrutiny".[119] In other words, he did not repudiate empirical and experimental natural inquiry. To Humboldt, aesthetics complemented rationality; it did not make it redundant. The mathematical precision of the stars' orbits was just as valid a topic for study as their sparkle and its associated delights.

The Romantic movement was, as Mannheim has demonstrated, associated with the reaction to the Enlightenment and the French Revolution.[120] Its repudiation of rationality was a response to the claims for the power of reason made by the radical philosophes. Goethe, Schiller, Schelling, and Hegel were all in their different ways conservatives.[121] Their attitude to nature and to natural inquiry was part and parcel of their conservative ideology. But Humboldt was famous in Paris, and notorious in Prussia, for his liberalism.[122] He was liberal in the liberal-conservative tradition which was prevalent, for instance, at the University of Göttingen. He favoured progressive reform by enlightened aristocratic government; he campaigned for the abolition of slavery; he supported moves toward the independence of the Spanish Colonies. But he opposed democratic institutions. A commitment to natural science was part of this liberal-conservative ideology.[123] Liberal elements in Paris, with which Humboldt identified himself, likewise did not participate in the repudiation of actively manipulative scientific inquiry.[124] Humboldt shared certain interests with Goethe and Schiller - but his view of society and the structure of the state was different from theirs. The divergent attitudes to science reflect this.

It is important here to note that conservative Romanticism, Mannheim's famous characterisation of its distinctive style of thought notwithstanding, did not have a monopoly on holism. There was a wide variety of holistic intellectual strategies available at the end of the eighteenth and the beginning of the nineteenth century. For instance, Neo-classical theory of Art, Blumenbach's Kantianism,[125] and the popular science sponsored by the Jacobins,[126] to take examples from strikingly different provenances, might all be said to be equally as holistic as the thought of Goethe or Hegel, in the sense that they all stressed unities and harmonies in nature, regarded particulars as meaningful only when they existed within an established framework, and held the mechanical system to be insufficient, in one way or another. A holistic stress on organic cohesiveness in nature and underlying regularities between phenomena may be taken as structural within the prevailing episteme.

Thus physico-mathematical empiricism, experiment and quantification could be harnessed to the construction of a universal holistic natural philosophy just as readily as were the intuitive and speculative efforts of Schiller and Schelling. The work of Blumenbach, Treviranus and Keilmayer, at the University of Göttingen, provides good examples of this being done in practice.[127] Likewise Humboldt effortlessly combined a commitment to empiricism and the experimental elucidation of the laws of nature with an equally strong commitment to holism and to a view of nature which was intended to be aesthetically and spiritually satisfactory.[128]

At several points in this chapter mention has been made of similarities between Humboldt and scholars associated with the

University of Göttingen. It seems appropriate at this stage to look more deeply into this connection. Fortunately we are greatly aided in this task by the detailed study of the University of Göttingen and its 'transcendental' style of Naturphilosophie which has recently been produced by Timothy Lenoir.[129]

Göttingen was the premier centre of scientific scholarship in Germany throughout the eighteenth century. In the 1780s and 1790s, scientific practice at Göttingen supported Kant's philosophical prescriptions in several ways. Göttingen scholars enthusiastically agreed with Kant's critique of teleological judgement and sought, like Kant, to harmonise the teleological with the mechanical viewpoint in the conceptualisation of organic entities. Biological organisms were conceived of as being objects within which the parts were bound together in such a way that cause and effect were mutually and reciprocally related - that is to say, effects participated in their own causation. This is virtually Kant's definition of holistic organisation. The Göttingen scholars also shared Kant's concern with the effect of the total environment upon the organism.

As he was a young man interested in natural science, it is understandable that Humboldt, at the age of nineteen, came to study at Göttingen.[130] If he and not his mother had been in charge of directing the early stages of his education, he might have got there sooner. As it was, although he remained there for only a year, in latter life he referred to the University of Göttingen as where he received the most valuable part of his scientific education.[131] He was a student of Blumenbach.[132] It is not surprising therefore that Lenoir has identified Humboldt as a major practitioner of the Göttingen style.[133]

Certainly there were many points of similarity between Humboldt's practice and that institutionalised at Göttingen. In his early experimental work on animal magnetism, Humboldt employed a conception of vital principle congruent with Blumenbach's Bildungstrieb - that is a vital teleological agency emergent from the organism's material substance.[134] Overall, Humboldt's view of the organism was very similar to that outlined above as being typical of the Göttingen school. It was likewise reminiscent of Kant's Critique of Teleological Judgement.[135] And, as we have seen, Humboldt applied the holistic teleological interpretation not only to individual organisms but to the supra-individual phenomenon of vegetation. Here we can also recognise elements shared with Blumenbach. Blumenbach had long been concerned with the effect on the organism of its total environment (what he called its habitus) and with the geographical distribution of natural phenomena.[136] His interest likewise ranged from the distribution of plants and animals to that of the moral characteristics of the races and peoples of mankind.

However it is likely that Lenoir both identifies Humboldt too strongly with Göttingen and over-emphasises the uniqueness and importance of the Göttingen programme and its achievements. Humboldt was, as we have seen from his connections with Goethe and Forster, a most eclectic thinker. And much of what Lenoir identifies as distinctively a product of Göttingen was present elsewhere - even in France.[137] The important point is, however, that much of Humboldt's cognitive concerns, particularly his holistic approach to the organism, to landscape and to Nature, were not unique to him. They were part of a much larger, institutionalised and socially sustained pattern of intellectual activity. It was not only Humboldt who effortlessly combined a commitment to empiricism, quantification and experimentation within a holistic framework.

Empirical investigation of the environment of plants

It must be emphasised that Humboldt's plant geography was a thorough empirical investigation of the environment of plants. As Humboldt wrote:-

> " ... it would be injurious to the advancement of science to attempt rising to general ideas, in neglecting the knowledge of particular facts."[138]

In his gathering of facts Humboldt made intensive use of instruments to measure physical parameters. One of the purposes of his scientific travelling was to measure accurately, with instruments, where previous explorers had merely described.[139] Subjective impressions were not themselves sufficient as "pointers to the Incommensurable" and isolated facts, however objective, were liable to mislead by giving only a partial impression of nature.[140] The intensity of the azure of the sky was not only to be appreciated aesthetically: it was measured and the measurements were tabulated and compared of different places. Likewise with the chemical composition of the air, its temperature, its humidity, its electrical conductivity, the barometric pressure, the boiling point of water, the dip of the magnetic needle, and much more beside. Virtually anything measurable was measured.

This enthusiasm for instrumentation and environmental measurement, although developed by Humboldt to an unprecedented extent (so much so that Cannon identified it as the distinguishing feature of Humboldtian science), did not arise de novo with Humboldt.[141] Nor was he the first to employ it as part of the practice of scientific travelling. The elder Forster measured the temperature of hot springs in Tahiti, the salinity of sea-water in various parts of the Pacific, and much else besides.[142] Of course, in those days, astronomy and navigation were the joint epitome of accurate measuring. It is, thus, no coincidence that many of the instruments taken by Humboldt to South America were navigational instruments - sextants from London, dipping needles from the French Board of Longitude.[143] He was adopting and adapting the tools and skills of the navigator and the surveyor. And British navigation, in its turn, owed much to the methods of terrestrial and celestial measurement developed by the German astronomer and geographer Tobias Mayer (also a professor at Göttingen and also interested in the regional differentiation of the earth's surface).[144] Quantitative studies of the physical environment were also part of the practice of science in Humboldt's adopted country, France. In his essay on the "Distribution of heat over the globe", Humboldt referred to observations made by Arago at the French National Observatory, and by Gay-Lussac during his famous ascent in a balloon.[145] Immediately on his return to Paris from the Americas, Humboldt collaborated with Biot on a study of geographical variation in magnetic intensity in which observations he made in South America were combined with others made by Biot in southern France, Switzerland and northern Italy.[146] Thus Humboldt's interest in environmental quantification again exemplifies his taking up pre-existing elements from his cultural and intellectual milieu, and his pressing them into service for his own ends.[147]

In Humboldt's plan for plant geography, all the different sorts of data from many different observation sites were to be tabulated and then correlated with the distribution of types of vegetation. Such correlations would aid the discerning of the laws which governed the distribution of vegetation. To facilitate these correlations, Humboldt developed the isoline technique of cartography.[148]

The vegetational regions of the globe

Humboldt's "magnificent lines"[149] enclosed not only areas of equal mean temperature and pressure but, in principle at least, defined areas of uniform vegetation - natural vegetational regions, characterised by distinctive plants. These regions possessed not just horizontal unity - they were not simply distinguishable one from another. They also possessed vertical unity. Indeed the reason they were horizontally distinguishable was because of the different integrative processes going on within each one. The vegetational regions are thus real natural wholes in contrast to the isolation of herbarium practice, the dried specimens upon which floristic taxonomy was based. They are identifiable by physiognomy. They were "non dans les serres et dans les livres de botanique, mais dans la nature même".[150] And the real wholeness of these regions was expressed at levels other than that of the vegetation. The regions were not simply vegetational units, but natural divisions of the earth's surface. They were, for example, also units of climate and of human activity. The "Tableau Physique des Régions Equinoctiales" represents in pictorial form one of these divisions - in this case the equatorial region of South America - in its unified interrelatedness and complexity:-

> "La même tableau indique: La végétation; Les animaux; Les rapports géologiques; La culture; La température de l'air; Les limites des neiges perpétuelles; La constitution chimique de l'atmosphère; Sa tension éléctrique; Sa pression barométrique; La décroissement de la gravitation; L'intensité de la couleur azurée du ciel; L'affoiblissement de la lumière pendant son passage par les couches de l'air; Les réfractions horizontales, et le degré de l'eau bouilante à différentes hauteurs."[151]

Natural regions of this sort were not, however, imagined to be topographically or vegetationally homogeneous. The "Tableau" also pictorially represents spatial differentiation within a single region. This last point must be grasped if we are to understand the topographical extent of the vegetational entities with which Humboldt dealt. A region might be defined by, say, the limits of natural occurrence of the palm tree. But within the region so distinguished, palm trees would not be distributed uniformly. On the tops of the mountains one would find a "région des lichens" or, lower down, a "région des Cinchona".[152] So within the natural region identified by the extent of the palm tree, other vegetational regions would have to be recognised. And vegetational features similar in character to these regions could be found elsewhere, even outwith the limit of the palm. Sweden, for example, was known to have regions of lichens, not quite so high on its mountains and thousands of miles from the nearest palm tree. Both these sorts of units, the ones which were of a single place and the ones which recurred within different geographical regions, were the expressions of environmental influence:-

> " ... and in the same manner as the perpetual snows are found in every climate at a determinate height, the febrifuge species of the quinquina (cinchona) have also their fixed limits."[153]

Both revealed patterns in nature. Both units were part of the subject-matter of Humboldtian plant geography.

The larger units might be regarded as coinciding, broadly speaking, with the biological provinces of the floristic botanist. Humboldt's technique of 'Botanical Arithmetic' was used to quantify floristic differences between the provinces.[154] There were other ways in which Humboldt's concerns coincided with those of the floristic phytogeographers at this level. However the study of the smaller, recurring unit was truly novel and unique to Humboldtian science.

The smaller sorts of vegetational region were often distinguishable by physiognomy - by the gross patterns of vegetational growth. Such patterns were the product of distinctive life-forms of plants:-

> "Dans la variété des végétaux qui couvrent la charpente de notre planète, on distingue sans peine quelque formes générale auxquelles se réduisent

la plupart des autres, et qui présentent autant de familles ou groups plus ou moins analogues entre eux. Il me borne à nommer quinze de ces groupes dont la physionomie ... "[155]

Examples of the classification of life-form used by Humboldt are:- the grasses, the palms, the cacti, the conifers, the lianes, the horse-tails (Equinetales), the mosses, and the lichens.[156] Thus the "régions des lichens" were distinguishable by the obvious profusion of a number of species, all with the same lichenous life-form:-

"For as in some individual organic being we recognize a definite physiognomy and as descriptive botany and zoology are strictly speaking analyses of animal and vegetable forms, so also there is a certain natural physiognomy peculiar to every region of the earth."[157]

This aspect of Humboldt's work on vegetation constitutes one of the most decisive ways in which he departed from floristic taxonomic methods. Classification by life-form, athough it did in many cases approximate to more orthodox taxonomies, was proclaimed to be independent of floristic systems:-

"In determining those forms, on whose individual beauty, distribution and grouping, the physiognomy of a country's vegetation depends, we must not ground our opinion (as from other causes is necessarily the case in botanical systems) on the smaller organs of propagation ... but must be guided solely by those elements of magnitude and mass from which the total impression of a district receives its character of individuality. Among the principal forms of vegetation there are, indeed, some which constitute entire families, according to the so-called 'natural systems' of botanists ... The systematising botanist, however, separates into different groups many plants which the student of the physiognomy of nature is compelled to associate together."[158]

Likewise, species closely allied for the taxonomist might be put into different life-form classes by the Humboldtian. For instance, herbaceous and arborescent members of the same genus would be so separated. The life-form classification was not proposed as a rival to the several post-Linnean natural systems. It served a different purpose, organising and describing natural phenomena from a different point of view. It did not concern itself with the relation of species but with identifying the "regions [which] form the natural divisions of the vegetable empire."[159]

Humboldt's concern with physiognomic life-form connects with the attempt of other German naturalists such as Blumenbach to construct ideal typologies:-

> "The primeval force of organization, notwithstanding a certain independence in the abnormal development of individual parts, binds all animal and vegetable structures to fixed ever-recurring types."[160]

Such a programme was present in both the transcendental and the speculative/metaphysical traditions of Naturphilosophie. But to the speculative Naturphilosophen such as Goethe, Oken or Carus, as Lenoir has observed, the Urtyp was the starting-point of a series of transformations producing a set of related forms.[161] To Blumenbach and Treviranus, the types or Grundformen represented plans of functional organisation.[162] This latter sense is the way in which the idea of physiognomic life-forms was used by Humboldt.

Humboldt's studies of life-form began the development of one of the major techniques for the classification of vegetation - a technique which was to form the basis of an enduring tradition of ecological research, throughout the nineteenth and into the twentieth century - classification by physiognomy.[163] The method was employed and elaborated upon by one of Humboldt's closest intellectual disciples, August Grisebach, who extended Humboldt's system to comprise fifty-four classes of physiognomic plant types (Vegetationsformen).[164] In 1872, in his Die Vegetation das Erde nach ihren Klimatischen Anordnung, Grisebach, with this technique, produced the first comprehensive classification of the world's vegetation.[165]

Social plants

Closely allied to Humboldt's interest in vegetational features of the kind represented by the "régions des lichens" and the "régions des Cinchona" was his interest in what he termed the "social plants":-

> " ... plantes, réunies en société comme les fourmis et les abeilles, convient des terraines immense dont

elles excluent tout espèce hétérogène."[166]

Examples of vegetational features produced and typified by the occurrence of social plants were heaths, savannahs and, on a smaller scale, sphagnum bogs. Such features were identifiable entities not only because they possessed a unified physiognomy, but also because the more obvious plants were all of the same species or genus.

The phenomena of social plants had been discussed by botanists before Humboldt. Willdenow for example wrote:-

> "In a climate a singular diversity in plants may be observed, viz. some are sociable, as it were. Others remain solitary, or some are never found but in great numbers crowded together ... These gregarious plants often occupy great tracts of land. Common heath (Erica vulgaris) is often spread many miles."[167]

But there is a crucial distinction to be made between Humboldt's treatment of heath as a vegetational feature and that of Willdenow. To Willdenow the heath is Erica vulgaris. It is characterised by the occurrence of one and only one species. Although Humboldt defines a social plant as one which grows without other species being present in the same area, in practice his usage is somewhat different. To him the heathland is not simply where many plants of Erica vulgaris grow. The heath is rather an 'association' of several plants of different species, indeed of different physiognomic types, among which E. vulgaris is the most obvious, the most numerous. Thus he writes:-

> "Les bruyères, cette association de l'erica vulgaris, de l'erica tetralix, des lichen icmadophile et haematomma ..."[168]

It is not only in considering heaths that Humboldt regards the phenomena of social plants as being that of groups of different species occurring together and not simply the profusion of a single species:-

> "Quoique le phénomène des plantes sociales paroisse appartenir principalement aux zones tempérées, les tropiques en offrent cependent plusieurs exemples. Sur le dos de la longue chaine des Andes, à trois milles mètres de hauteur, s'étendent le brathis juniperina, le jarava (genre de graminées voisin du

> papporophorum), l'<u>escallonia</u> <u>myrtilloides</u>, plusieurs espèces de <u>molina</u> et surtout le <u>tourrettia</u> ... "[169]

Such assemblages are not simply "associations de plantes de la même espèces"; they are plant communities - types of vegetation.

Humboldt's listing of species occurrence, in the above way, may be readily distinguished from Willdenow's practice. Humboldt was characterising units of vegetation; Willdenow, units of flora. But it should be noted that Humboldt was, by listing constituent species, characterising vegetational units in floristic, rather than physiognomic, terms. The development of this technique (which utilised the traditional skills of taxonomically-trained field botanists) has led to another great tradition of vegetational research and classification - that based on floristic analysis - which existed (and still exists) side by side with the development of techniques based upon physiognomy.[170]

<u>Why a science of vegetation?</u>

We have now seen the broad outlines of the novel complex of cognitive interests which characterised late eighteenth- and early nineteenth-century natural history. We have also seen Humboldt's relation to this new <u>episteme</u>. We can now answer the questions posed at the beginning of this chapter. What brought into being a new form of scientific practice based on a new object (vegetation) - indeed new objects (vegetation units) - for scientific inquiry? Why, at this particular point in time, did an independent study of vegetation arise?

A concern with natural regionality was a prominent feature of the intellectual activity of the age. This was expressed in botany in the development of both floristic and vegetational plant geography. The study of plants could readily accommodate a concern with regionality since the distribution of vegetation was one of the most striking aspects of the differentiation of the earth's surface. Also vegetation could itself be subdivided into smaller, more esoteric, natural units. The late eighteenth-century concern with regionality produced the ideas of the regional Flora and the unit of vegetation.

The new *episteme* was holistic and presupposed organic cohesiveness and regularities underlying visible phenomena. Philosophers and natural scientists were also concerned with constructing environmental explanations for the structure of biological organisms and the character of human societies. Here again the study of vegetation offered botanists excellent opportunities to conform with new cognitive trends. The study of vegetation seemed to transcend the limitations of Linnean botany by addressing itself not to what were seen as arbitrarily isolated entities, but to real natural wholes. Vegetation and the relationship between vegetation and the physical environment were both eminently conceivable in holistic terms. And vegetation was not only itself an expression of the total environment, it could be regarded as one of the aspects of any given environment that most affected Mankind.

For this last reason, the students of vegetation could claim shared aesthetic concerns with contemporary landscape painters and nature poets. The study of vegetation had common resonances with *Naturphilosophie*. It was not narrowly or coldly scientific but spiritually rich and fulfilling. Furthermore, accounts of exotic vegetation were contributions to the literature of travel. The study of vegetation thus offered a route towards professional acceptability on a wider cultural stage.

But it did not lack conventional trappings of objective science - as science was then conceived. It did not lack scientific respectability. Here the study of vegetation had a tactical advantage over the study of floristics. Both could readily employ quantification. But vegetation science with its interest in the physical environment of plants could more easily make use of measuring instruments. It could more easily accommodate the compilation of physical data on a grand scale, the correlation of one physical parameter with another, the search for universal natural laws. Furthermore the idea of natural kinds of vegetation identifiable by physiognomic type was congruent with an emphasis on the construction of ideal typologies - again an important component of the intellectual activity of the time.

Thus the changed intellectual climate made the study of vegetation feasible, if not quite inevitable or unavoidable. The need for natural historians to respond to changing scholarly circumstances made the study of vegetation attractive and convenient. But congruence with wider cognitive trends was not enough in itself, to guarantee an enduring place for the study of the novel object of the plant community within scientific practice. The important point here is that the recognition of plant communities as entities within vegetation gave botanists new, interesting and scientifically respectable things to do. They could go out into the field to identify, map and classify plant communities. If they were working on a small scale, in areas in which the flora was already well investigated, botanists could utilise the taxonomic skills they already possessed and characterise the units of vegetation by floristic criteria. If they were working on a large scale, where floristic analysis would be too cumbersome, or in an area as yet floristically unexplored, they could classify the vegetation using non-floristic physiognomic criteria. Furthermore, refining and elaborating the bases of physiognomic classification was itself a viable research activity.

The study of the units of vegetation gave botanists useful things to do when they travelled - as they were supposed to do. Indeed all Humboldt's expeditionary publications functioned as exemplifications of how to accomplish the difficult and important task of making a scientific journey. Humboldt provided exemplars as to what, how and why the botanical explorer was to observe and investigate. Of course Humboldt's travel narratives inspired and influenced many workers perhaps not directly in the Humboldtian mode such as Darwin, Joseph Hooker and the explorers of the American West.[171] But his writings were also, more immediately and directly, models for a considerable number of botanists (mostly German or Scandinavian) who went out into the field to identify and study the types of vegetation. In other words, around the exemplar of Humboldt's treatment of vegetation, there developed a new research specialty - Humboldtian plant geography.

The remainder of this chapter is devoted to examining the emergence of this new form of scientific practice. I have already described paradigm development. I will now go on to describe paradigm articulation, mediated by personal communication and recruitment.[172]

The Humboldtians - Schouw and Meyen

Humboldt was the first to call communities of plants 'associations'. Humboldt used the term 'association', as we have seen, informally - "Les bruyères, cette association de l'erica vulgaris ... ", or to take another example, "I have explained the first ideas of the geography of plants, their natural associations and the history of their migrations ... "[173] But the term 'association' soon became a technical one meaning a definite and distinguishable plant community. Around the term an extensive technical vocabulary grew - as a body of practice and practitioners of Humboldtian plant geography developed.

Humboldt never held an academic position so he had no students as such.[174] But as well as the exemplars which his published works provided, he exercised influence through a vast scholarly acquaintance and considerable academic patronage.[175] He maintained an immense scientific correspondence.[176] Joachim F. Schouw, for instance, read and was inspired by Humboldt's work in the early 1810s, when he was abandoning a career in law and training to become a botanist.[177] He was applying Humboldtian principles to the understanding of the vegetation of Scandinavia by the end of the decade. This is indicated by the title of one of his first publications:- "Einige Bemerhungen uber zwei, die Pflanzengeographie betreffende Werken des Herrn von Humboldt".[178] Schouw corresponded with Humboldt and in 1819 journeyed to Paris to meet his mentor.[179]

Schouw made his visit to Humboldt on the way back from a trip to Italy. He visited Italy again in 1829. He later published an account of these scientific travels.[180] In his introduction to this work he apologised for his delay in producing an account of his voyages. This he said was due to his absorption with such Humboldtian concerns as:-

> " ... son traités sur la géographie universelle des plantes et son tableau du climat du Danemark."[181]

Schouw's own descriptions of his work illustrate how similar his concerns are to Humboldt's. He investigated the physical environment to correlate it with the distribution of vegetation, to create "la géographie universelle des plantes":-

> "Le volume actuel [the first] contient le tableau de la temperature et des pluies, et comme la configuration du sol exerce une influence essentielle sur le climat ... Le second volume contiendra les autres élémens du climat et une comparaison des années diverses relativement au caractère météorologique, ce qui conduira aussi à traiter la question intéressante des variations qu'a attribue au climat. Le troisième volume sera consacré au tableau phytogéographique."[182]

The first volume is given over entirely to tables of physical measurement:-

> "Le climat et la végétation sont influencés puissamment par l'élévation du sol au-dessus de la mer, le but de mon voyage exigeoit par conséquent la determination de la hauteur d'un grand nombre de points."[183]

Schouw was also interested in the units of vegetation and, in 1822, he invented a nomenclature for associations which consisted of adding the suffix '-etum' to the generic name of the plant which dominated the given association; for example, 'Fagetum' for a community dominated by a species of Fagus, the beech tree, or 'Quercetum' for an association in which one of the species of the oak, Quercus, was the most numerous tree.[184]

Schouw developed both the floristic and the vegetational aspects of Humboldt's plant geography.[185] He is probably more famous for his work on the floristic side.[186] His approach to plant communities was, as we can see from his nomenclature, primarily floristic. However, that was not the whole story of the Humboldtian legacy. In 1838, August Grisebach re-emphasised the physiognomic aspect and introduced the new term 'formation':-

> "I would term a group of plants which bears a definite physiognomic character, such as meadow, a forest, etc., a phytogeographic formation. The latter may be characterized by a single social species, by a complex of dominant species belonging to one family, or, finally, it may show an aggregate of species, which, although of various taxonomic character, have a common peculiarity; thus the alpine meadow consists almost exclusively of perennial herbs."[187]

Eventually it became conventional to use the term 'association', frequently together with the '-etum' nomenclature, to refer to vegetation types characterised by floristic criteria, and the term 'formation' to refer to types characterised by physiognomy, as in Grisebach's examples.[188]

Note that it is impossible to say when precisely the idea of the plant association first arose. To the question "Is the idea of the association present in Humboldt's writings?" one could give only an equivocal answer. His use of the term is, as we have seen, informal. He certainly spoke of natural regions of vegetation, but are they really associations in the later technical sense of the word? Only if one interprets Humboldt's text in the light of later work. On the other hand, to the question "Is the idea of definite plant communities present in Grisebach's work?" one would have to give, I think, an affirmative answer (with the proviso, of course, that usage has changed somewhat in the decades which separate Grisebach from twentieth-century ecology). When exactly between Humboldt's Essai and Grisebach's 1848 paper, did the concept of the association (or the formation) arise? I cannot answer this question. But this inability is not, I hope, caused by a failure of scholarly investigation. The situation of the origin of the plant community is very similar to that described by T.S. Kuhn in his account of the discovery of oxygen.[189] The identification of 'oxygen' as an entity in the real world was not a unit-event. Conceptual categories changed gradually as new scientific practices developed. Slowly, the category 'oxygen' emerged. So it was with the idea of the plant community. In reality, the plausibility of its being part of the structure of the world, increased as more people investigated it and found the concept useful in the investigation of other things. So the reality of plant community, like the reality of oxygen, gradually emerged from a process of cognitive change. It developed with the articulation of a new programme of research.

In the work of Meyen, August Grisebach and Kerner von Marilaun, the Humboldtian programme for a plant geography based on a supra-individual, supra-specific unit was continued and developed. To gain the full character of the Humboldtian legacy as it was expressed in the scientific practice of the next generation, it is worthwhile looking briefly at these authors.

Franz J.F. Meyen was, until his death in 1840, Professor of Botany at the University of Berlin. He was one of the most favoured of Humboldt's many scientific protégés.[190] Meyen, who had been working as a physician when Humboldt returned to Berlin in 1826, owed both his scientific career and his post at the University to Humboldt. Humboldt took great trouble to make Meyen's work known to a wide audience and he personally sponsored Mirbel's French translation of Meyen's book on plant geography. This book was later translated into English as Outlines of the Geography of Plants.[191] It is one of the earliest, most successful and most explicit articulations of the Humboldtian exemplar.

One might almost say that Meyen's career is a replica in miniature of Humboldt's. Meyen, for example, travelled in the New World (1830-2) and recorded both scientific and aesthetic observations made on summits in the Andes:-

> "The sight of a little Gentian, very similar to our Gentiana uliginosa and G. nivalis at the height of 14,000 or 15,000 feet as in the Cordillera of Southern Peru, can enchain the botanist for hours; he again and again gathers this little plant which takes him, at least in imagination, home."[192]

Extant correspondence between Humboldt and Meyen indicates that Humboldt influenced his protégé's travel plans at every stage.[193] Meyen's botanical geography was explicitly presented as Humboldt's "new science which answers in a way that had before been impossible, many of the most interesting questions on the production and distribution of organic beings on the surface of the globe".[194] Humboldt's name was regularly invoked throughout Meyen's book.

Outlines of the Geography of Plants was, among other things, a sustained and sophisticated attempt to correlate vegetation with measured physical factors. Meyen employed copious instrumental records, mostly of his own making, drew up temperature charts and tables and employed isothermal, isotheral and isocheimenal lines to apply meteorological data in the study of the distribution of vegetation:-

"It is very easy to show that the conditions of climate, particularly heat and moisture, are the chief causes which determine the station and distribution of plants and therefore it is of the greatest importance to know exactly the modes in which the influence of the often extremely complicated conditions of climate become apparent. To arrive at this end, we must first ... employ ourselves with the observations which have been collected on the distribution of the heat and moisture of the atmosphere over the whole globe and which are by no means of pure meteorological interest but constantly point to the influence which individual meteorological phenomena exercise over vegetation."[195]

Meyen was interested in floristics and systematics but he had carefully distinguished floristic plant geography from vegetational plant geography, which interested him still more. In floristic plant geography his principal tool was the Botanical Arithmetic (or Statistics) of Humboldt, De Candolle and Schouw.[196] In the study of vegetation, however, he was principally concerned with classification by physiognomy:-

"The subject of the distribution of plants over the surface of the globe may be divided into two perfectly distinct branches, one of which called the Physiognomics considers vegetation according to the distribution of forms which point out the groups of plants; it is a peculiarly natural system in which similarity of form is the principle of classification ... The other branch, viz. the Statistics of plants on the contrary ... considers the relative proportions, founded on real numbers which this or that group by its number of species bears either to the whole mass of known plants or to the number of species of other groups."[197]

Meyen's plant geography extends Humboldt's Essai in every direction. He investigated the role of vegetation in Man's aesthetic appreciation of Nature:-

"Baron Alexander von Humboldt['s] ... celebrated work "Considerations on the Physiognomy of Plants" pointed out this highly interesting side from which botany may be viewed and how it may improve the taste of nations by increasing their sensibility to the beauties of nature and thus have an influence on the progress of the arts."[198]

He also considered the effect of vegetation upon human society, illustrating Humboldt's argument that the regionality of vegetation was both a reflection and a cause of the natural divisions of geographical phenomena:-

> "It is vegetation which fixes the natural character of a region and determines the conditions according to which men gather into various societies, at one time leading a nomadic life, at another enjoying more or less the beneficent influence of agriculture. Where vegetation is scanty, and man is more or less confined to animal food, as in the case of the Samoyedes and Esquimaux on the coast of the Northern ocean, civilisation is impossible. In those regions, man lives like the beasts and does not even think of rousing himself above them."[199]

August Grisebach

August Grisebach and Kerner von Marilaun were, like Meyen, close associates of Humboldt and self-consciously continued Humboldt's programme for a plant geography. Grisebach was born in 1814.[200] His early interest in botany was encouraged by his uncle, the eminent German natural historian Georg F.W. Meyer, who was a professor at the University of Göttingen. Grisebach was himself a student at Göttingen from 1832 until 1834 when he moved to the University of Berlin. In Berlin he was a student of Franz J.F. Meyen, and he became acquainted with C.S. Kunth, who had been the botanist principally in charge of the taxonomic work upon the specimens collected by Humboldt and Bonpland in South America.[201] Kunth was, therefore, although principally a taxonomist, one of Humboldt's closest scientific collaborators.[202]

In 1833 Grisebach went on a botanising trip to southern France. He had read Humboldt's accounts of his travels and was already interested in the types of vegetation characteristic of different regions and different environments. In 1839 he set out again on a major expedition into the hitherto botanically-unexplored regions of Thrace, Macedonia, Albania and Northern Asia Minor. He made a transect across the Balkan peninsula, reminiscent of the transect of South America pictorially represented in Humboldt's _Essai_. These travels were described in his _Reise durch Rumelian und nach Brussa im Jahre 1839._[203] This account contains much Humboldtian observation, particularly of altitudinal zonation of vegetation. For example, on the slopes of Ulu Dag, he described three main zones of vegetation:- the region of sweet chestnuts, the region of conifers, and the alpine region.

On his return to Germany he became _privatdozent_ at the University of Göttingen, rising to full professor in 1847. Another botanising and phytogeographical journey was undertaken, to Norway, in 1842. By this time Grisebach had become a personal friend of Humboldt and the two exchanged a copious scientific correspondence.[204] Grisebach became one of the leading exponents of Humboldtian plant geography and he wrote the chapter on Humboldt's work in plant geography for Bruhn's commemoratory _Life of Humboldt_.[205] Further displaying the Göttingen connection, Grisebach also wrote the laudatory account of Blumenbach in _Göttinger Professoren_.[206]

I have already referred to Grisebach's introduction of the term 'formation' to refer to "a group of plants of definite physiognomy" - for example an alpine meadow consisting almost entirely of perennial herbs. In 1838, he indicated the relation between physiognomic and floristic criteria by pointing out that a physiognomic formation could be characterised by a single dominant (social) species or by a number of dominant species of related taxa.[207]

Grisebach was an accomplished taxonomist and was interested in floristic as well as vegetational plant geography.[208] Indeed the two activities were held to complement each other:-

> "Banbury has made a report in his botanical travels in South Africa. His description of the character of the vegetation in the environs of Cape Town is so much the more interesting, as being accompanied by Harvey, who is intimately acquainted with the Cape Flora, he was enabled to acquire an exact knowledge of the species."[209]

A good example of Grisebach's approach to vegetation is afforded by his account of Blasius's description of the distribution of organic nature in European Russia:-

> "Northern Russia is chiefly distinguished from the central province by its dense forests, in which _Pinus sylvestris_, L., and _P. abies_, L., are the predominant species, and whose vast extent is only broken by swamps, or where, in the neighbourhood of the fluvial valleys, the trees have been thinned and destroyed by man. Amongst the pines and firs are intermingled here and there, _Alnus incana_, L., and _Betula pubescens_, Ehrb., which in some parts constitute by themselves

> large forests. The limits between cultivation and the wilderness are everywhere indicated, especially by alder bushes. Besides which the only form of leaf-trees are Populus tremula, L., Sorbus Aucaparia, L., and Prunus Padus, L. The pines and firs form two distinct forest formations, differing in the proportion of the argillaceous constituent of the soil. The clayey, often marshy low lands of the old red sandstone are covered with thick fir wood, among which occur the aspen and the alder; the sandy diluvial hillocks bear Pinus sylvestris, L., and Betula pubescens, Ehrb., and represent the forest character of the North German plain, the soil of which has been formed at the same time. On this diluvium, where the soil is deficient in clay, are met with also heaths of Calluna which do not occur in the Siluria plains and trap formations. However the diluvium is not altogether free from bog, where Ledum and Andromeda calyculata, L. flourish, but even here also, the fir ... does not grow, but only the pine ... which does not shun the water and requires only a light sandy soil."[210]

While farther south:-

> "The northern marsh willows are replaced by Salix fusca, L., Cinerea by Caprea L., and Alnus incona, D.C., is represented by Alnus glutinosa, G. Thus almost all the plant formations assume another character, but the physiognomy of the whole country is much more strikingly altered by the increased extent of cultivation."[211]

The last quotation in particular illustrates the relation of vegetational to floristic phenomena in Grisebach's work. The formations are phenomena in their own right, distinguishable by physiognomy, but they are also characterisable by the plant species which constitute them.[212]

Kerner von Marilaun

Kerner von Marilaun, Professor of Botany at the University of Innsbruck, wrote that due to the scientific travels of Humboldt more was known of the vegetation of South America than of Austria-Hungary:-

> "Attention was called to our native plant formations only when travelers with genius and good fortune showed in word and picture the marvelous plant formations which spread in primeval virginity beneath tropic suns along the banks of the giant rivers of South America ...

It is literally true that we have had exact descriptions and splendidly illustrated portrayals of the shores of the Pacific Ocean or the tropical zone of Brazil for a long time before our native plant formations were given a similar treatment."[213]

Kerner von Marilaun's task was to redress this imbalance using Humboldtian methods. He travelled extensively in the previously botanically-unexplored regions of eastern Hungary and Transylvania.[214] In the characterisation of vegetation his methods were physiognomic ones. He proposed a nomenclature for plant formations, based not on floristic criteria as Schouw's had been, but on physiognomy. He was careful to distinguish the study of physiognomy from the study of floristics:-

" ... almost every systematic group is represented by various forms which are totally different in physiognomy ... Plant physiognomy and plant systematics go entirely different ways."[215]

In the work of Grisebach and von Marilaun the opinion was expressed that the individual plant was fully understandable only if it was considered as a member of a distinct community. As well as being a unified response to the climate and other environmental factors, the plant community had a high degree of internal integration - which was part of the reason one community was readily distinguishable from its neighbours. Plants living together had effects upon one another and the character of vegetation was partly determined by these effects. The social groups of plants had a definite social structure.

As Kerner von Marilaun wrote in his classic text Das Pflanzenleben der Donauländer, published in 1863:-

"The horizontal and vertical assorting of large plant communities is by no means accidental in spite of its apparent lack of order. It follows certain immutable laws. Every plant has its place, its time, its function and its meaning ... In every zone the plants are gathered into definite groups which appear either as developing or as finished communities, but never transgress the orderly and correct composition of their kind. Science has given to such groups the name Plant Formations. With the comparative study of landscapes botanists found it necessary to define and characterize these ever-recurring elements which are so conspicuous in the physiognomy of landscape."[216]

Like Humboldt, von Marilaun was also concerned to understand the vegetation as an expression of the physical environment:-

> "Everywhere plant life is adjusted to the local climatic conditions. When one opens the great green Book of Nature, one finds therein the local climatic conditions generally much more precisely and correctly registered than on the yellowing pages of thick meteorological journals and folios. The vegetation is everywhere the reflection of the local climate. For that reason no feature of the landscape is so significant and informing as the vegetation."[217]

Also, like Humboldt, Kerner von Marilaun regarded the study of vegetation as bearing upon the entire range of human activities:-

> "What a wealth of problems arise in investigating the relation of these different expressions of landscape to the spiritual side of Man, to his feeling toward nature, to his culture and to the products of his creative art."[218]

It is clear from Das Pflanzenleben der Donauländer that by the middle of the nineteenth century, much more was known about vegetation than when Humboldt wrote his essay. Marilaun's descriptions of the plant formations of Austria-Hungary are very detailed - his accounts of plant succession, what he termed "the genetical relationships of plant formations", are particularly well-observed.[219] He could confidently point to several instances where the study of vegetation had proved its practical utility to fields such as forestry. But the framework of inquiry is recognisably Humboldtian.

Southern Humboldtians - Lecoq and Heer

By the mid-nineteenth century the study of plant communities, natural kinds of vegetation, was well established in scientific practice. As well as the workers already mentioned, explicitly Humboldtian concerns were evident in the work of many other German and Scandinavian authors. Important examples of texts in this tradition are those of Heer, Thurmann, Sendtner, Lorenz and Hult.[220] These men were, like Grisebach and von Marilaun, the bearers of a Humboldtian tradition of plant geography and the users of the idea of the plant community.

A keen interest in the phenomena of vegetation is also displayed by the advanced and wide-ranging work of the French botanist Henri Lecoq, Civic Professor of Natural History at Clermont-Ferrand.[221] Lecoq's allegiance to Humboldt is clear:-

> "Mais alors un livre me tombe sous la main; j'avais appris, quoique bien jeune encore, à respecter le nom de son auteur, et ce livre, en me révélant une science que je soupçonnais sans la connaître, mit de l'ordre dans mes idées; et dirigea par la suite une partie de mes études; c'etait L'Essai de Geographie botanique du célèbre Alexandre de Humboldt."[222]

Lecoq, like Meyen, made a firm distinction between flora and vegetation:-

> "Il y a donc une tres-grande différence entre La flore et le tapis végétal d'une contrée. La première fournit les matériaux qui servent à constituer le second."[223]

Like Humboldt, Lecoq found the geography of plants of more interest than floristic botany:-

> " ... j'ai dû autant que possible, conserver les anciennes espèces, en les considérant, au besoin, comme des groupes. Je n'ai pas l'intention de publier une flore ni de discuter des charactères, mais seulement de m'occupe de la géographie et de la dispersion des espèces du plateau central de la France. Ce n'est donc ni par ignorance des Ecrits publiés, ni par négligence ou mauvais vouloir, que je n'adopte pas la majeure partie des espèces nouvelles; j'apprécie mit le mérite des botanistes qui se livrent à cette étude, mais, pour des travaux de géographie botanique, je suis forcé de me contenter souvent des groupes au lieu d'espèces bien définies."[224]

In his enormous eight-volume treatise on the vegetation of central and southern France, Lecoq described many different associations. The distribution of the associations was correlated with climatic and environmental factors such as the intensity of solar radiation, temperature, soil water content, and so on.[225] Lecoq also gave a theoretical discussion of the vegetational phenomena of 'sociabilité' (many plants of the same species living together) and 'association' (many plants of different species living together).[226]

Of course it must be admitted that not every botanist who acknowledged the influence of Humboldt was a Humboldtian plant geographer in the sense I am using that designation. A passage in praise of Humboldt very similar to that I have quoted from Lecoq occurs in the introduction to Alphonse de Candolle's great book Géographie Botanique Raissonnée.[227] What distinguished the tradition of Humboldtian plant geography from that of floristic plant geography was the concern for vegetation. De Candolle correlated plant distribution with climatic, physical and geographical factors, but all throughout the book he was concerned with the distribution of species, genera and families, hardly at all with vegetation types. It is significant, for instance, that the illustration folded into the first volume of Géographie Botanique Raissonnée is not a Humboldtian panorama of natural regions and vegetation types, but a map of the northerly limit of various plant species in Europe.

De Candolle recognised the existence of what he called Topographie botanique, which he defined, partly, as:-

> " ... rechercher quels sont les charactères de la végétation des marais, des prairies, des forêts, etc., dans quelles proportions les diverses catégories de plantes s'y trouvent représentées, par quels motifs certaines espèces en sont exclues, etc.; ce serait une Topographie botanique."[228]

But he was not very interested in pursuing that study:-

> "Cette distribution locale, ou topographie des plantes, pourrait constituer une branche de la science, moins importante sans doute que la geographie botanique, mais offrant des développements analogues ... Mon intention n'est pas d'en parler ici fort en détail, car se serait sortir de mon sujet."[229]

De Candolle personified the floristic side of the dichotomy of emphasis which existed in nineteenth-century plant geography.[230]

The floristic style of botanical geography seems to have been the most popular in France and Britain. Watson, Hooker, Wallace and Darwin (as far as his plant geography was concerned) all practised a form of investigation principally structured around the problems of distribution and dispersal of species.[231] There appear to have been few nineteenth-century British plant geographers who placed great emphasis on vegetational phenomena.[232]

However, in the German-speaking countries and Scandinavia, the Humboldtian example of the study of vegetation seems to have been widely adopted. [There were, of course, many floristic plant geographers in Germany and Scandinavia also.] It is instructive, for example, to compare Richard Hind's account of his botanical observations during the voyage of H.M.S. Sulphur with the roughly contemporaneous work of Oswald Heer, Professor of Botany at the University of Zurich.[233]

Despite the title of Hind's book - The Regions of Vegetation - his regions are somewhat arbitrary geographical divisions - the Japan region, the China region, the Birmah region and so forth. His description of these regions, apart from brief remarks as to the general character of the landscape, are entirely floristic. Only in the description of the "Himma-leh region" does he depart from this procedure. Here, with a bow, as it were, to Humboldt's description of the Andes, he recognised the "region of lowland cultivation", the "region of woods", the "region of shrubs", the "region of grasses" and the "region of cryptogamic plants".[234]

Heer's emphasis, on the other hand, was almost entirely vegetational. Folded in at the end of Heer's Beitrage zur Pflanzengeographie is an engraving of a mountain panorama, entitled "Gemälde der Vegetation des Südöstlichen Theils des Canton Glarus", which is strikingly reminiscent in size, style and content, of Humboldt's "Tableau Physique". Accompanying the engraving is an elaborate table indicating the physical environment of each region depicted. Characteristic soil and atmospheric temperatures, for instance, are given. A key to symbols on the picture gives the most important species to be found in each region. For instance, the rocks of the upper zone of the regio nivalis are said to support a vegetation characterised by saxifrages and Primula.

Heer was careful to distinguish his approach to plant geography from that of the more floristic Linnean botanist Wahlenberg:-

> "Ich suchte auf diesen Reisen mir geuane Verzeichnisse von den Pflanzen aller Höhen und Localitäten zu verschaffen, wobei ich die Methode von Schouw befolgte ... Die Methode Wahlenberg fand ich sehr unzweck mässig ... "[235]

Northern Humboldtians - Hult

The work of the Swedish botanist, Hampus van Post likewise exemplifies the distinction between vegetational and floristic plant geography. He frankly criticised his fellow Scandinavian botanists for not adopting the physiognomic approach - criticisms which earned him some censure from his peers.[236]

Of the later Scandinavian Humboldtians the work of Ragnar Hult is particularly interesting to look at, since his approach and methods were further developed by Rutger Sernander under whose leadership the Uppsala school of plant sociology was founded.[237] The Uppsala school was to be one of the two dominant schools of plant ecology in Western Europe throughout the twentieth century - the other being the Zurich-Montpelier school founded by Flahault and Schröter. Sernander was an assistant of Hult in the early 1880s and Du Rietz, Osvald, Nordhagen and L. von Post were all students and disciples of Sernander.[238] Thus in Hult we see a direct link between the practice and usage of what I have termed Humboldtian plant geography and the 'self-conscious' ecology and plant sociology of the twentieth century.[239]

We can see Hult's debt to Humboldt as far as the style and content of his work in the introduction to his important article "Försok till Analytisk Behandling af Vächstformation" (Attempt to make an analytical scheme of plant formations).[240] For instance, Hult shared Humboldt's stress on units above that of the individual plant species and his concern for an aesthetic as well as a scientific response to vegetation:-

> "When botanical geography first appeared, it was an appendage and auxiliary to systematic botany. Species, genus, families and higher taxa were studied from the point of view of site conditions, distribution and mode of distribution and from this research conclusions were drawn regarding each taxon's habitat and so on. It was ignored or overlooked that there also existed other individually very obvious groups of plants as well as the systematic taxa, "one did not see the wood for the trees".
>
> It needed Humboldt's mighty spirit ... to discover these groups and to realize their immense significance in the geography and history of the Earth. In his travels through tropical America he was struck by the

definite outlook which certain characteristic and dominant plants lent the landscape. He saw the shifting expression of this outlook in the dark of the jungle and on the monotonous plains of the savannas, on the palm decked tidal beaches, and in the treeless high mountains of the Andes; he saw the vegetation of all the regions together within a limited space, but organized according to a system of law which he could not fail to notice ... he emphasised primarily the physiognomy and the growth forms of plants, the interdependence of these features from systematic relations, and their role in the character of the landscape, as well as these group's mode of growing together, the monotony of the colonies of the social plants in contrast to the diversity of forms and variations in the tropical jungle."[241]

Hult thus clearly and explicitly identified himself as working within the Humboldtian tradition. However he adopted only some aspects of the Humboldtian legacy - its emphasis on physiognomic forms and the identification of vegetation units, for example - and discarded others - notably environmetry. By the second half of the nineteenth century, Humboldtian plant geography had suffered several internal divergences in the process of its development as a research tradition. Hult distanced himself from the work of Schouw for example, whose approach to plant communities he regarded as deductive - by which he meant principally concerned with the environment rather than the vegetation itself - and unduly floristic.[242] Hult's approach was strictly physiognomic.

Some of the different manifestations of the Humboldtian tradition had, as in Hult's case, characteristics which their direct lineal descendants were to continue to display in the era of self-conscious ecology and plant sociology. For instance, in Hult's work we see preoccupations that are to become quite characteristic of the Uppsala school - a concern to study the vegetation as an end in itself rather than as an expression of the habitat, and a concern with very small units of vegetation:-[243]

"Because if one is to go for example to a moor in the middle of Finland, one can see there in an area where no differences in the chemical or physical conditions can be shown at least two sharply divided plant groupings alternating in patches. One is an even and dense mass of _Cladina silvatica_, with other lichens sprinkled in, as well as _Polytricha_ and low _Empetrum_; the other is a similarly thick and even mat of Calluna vulgaris, with a sparse undergrowth of Cladoniaarter, Hylcomia and Polytricha, as well as sparse and blended clumps mixed in of Hieracium umbellatum, Solidago, and a few other plants. Here we can thus see an intimate mixture on the same location of two plant communities, which are in sharp contrast to each other. And these have to be united by the deductive school of thought, which according to the varying degrees of dampness of the soil, distinguishes formations with barely distinguishable vegetation."[244]

The emergence of a 'self-conscious ecology'

The process by which ecology became institutionalised and recognised as a discipline in its own right, is beyond the scope of this thesis. However all commentators are agreed that this process may be said to have been well under way, at least in Europe, by the time Warming, Drude and Schimper produced their great summary volumes in 1895, 1896, and 1898 respectively.[245] Also, by this time Flahault and Schröter had laid the foundations of the Southern or Zurich-Montpelier school of plant sociology.[246]

The work of all these men bore the mark of the Humboldtian tradition.[247] Their investigations possessed much of the character they did because Humboldt and the Humboldtians lived and worked before them. Schröter, for example, was a doctoral student of Oswald Heer's at the University of Zurich.[248] He was a sufficiently favoured student to inherit Heer's professorship upon Heer's death in 1883. Schröter's biographer and student, Eduard Rübel, has stressed the influence of Kerner von Marilaun's Pflanzenleben der Donauländer upon Schröter's early phytogeographical work.[249] Kerner's Pflanzenleben provided an important model for Schröter's own Das Pflanzenleben der Alpe. Thus we see that the Zurich-Montpelier school, like its northern counterpart the Uppsala school, had, through its founders, direct student-mentor links to Humboldt and the early Humboldtians.

Warming's and Schimper's books were of immense influence in Britain and North America as well as in Germany and Scandinavia. Two of the principal preoccupations of Schimper's book are already well known to us - concerns we have identified as clearly belonging to the Humboldtian tradition. Schimper structured his treatment of the world's plant cover around a classification of vegetation into region, formations and smaller units. This classification was, at least largely, physiognomic:-

> "Climatic formations may be traced back to three chief types - woodland, grassland and desert. Woodland is constituted essentially of woody plants, and is termed forest if trees grow in a closed condition; bushwood when shrubs are so abundant as to keep the crowns of the trees from touching one another; shrubwood where shrubs constitute the chief feature."[250]

Secondly Schimper wished to correlate the occurrence of vegetation types with the physical environment. His book is replete with tables of mean temperatures in the Brazilian forests, humidity in the antarctic, the variation of day-length with latitude - all manner of physical data from all the major vegetational regions of the world. Schimper was the first to make a distinction between two forms of environmental control which was to be of lasting importance in the development of plant ecology:-

> " ... two oecological groups of formations should be distinguished - the climatic or district formations, the character of whose vegetation is governed by atmospheric precipitations, and the edapic or local formations, whose vegetation is chiefly determined by the nature of the soil."[251]

Folded in at the end of the book are a set of maps showing the distribution of the world's rainfall, correlated with the occurrence of the climatic vegetation-types.[252]

There are many novel elements in Schimper's work. The years since 1850 had seen many changes occur in German botany. Botany had, with the development of plant physiology, become more experimentally orientated and less holistic.[253] The problem of adaptation, conceived anew in Darwinian terms, altered the character of studies into the external and internal structure of plants. However the new trends in botanical science did not swamp the older programme of Humboldtian plant geography. Rather they interacted with it to produce the new style of investigation that was to be called 'ecology'.

The publication of Grisebach's Die Vegetation der Erde stimulated many botanists to study the relationship between vegetation and environment.[254] For instance, the anatomist Schwendener assigned to a doctoral student the task of determining whether the vegetation zones described by Grisebach were reflected in anatomical differences between plant species.[255] Grisebach was staunchly anti-Darwinian.[256] But, generally, those who applied the fruits of the new study of physiology and morphology to understanding the life of the plant in the wild were concerned with interpreting structure and formation in Darwinian terms.[257] Thus, after Grisebach, vegetational plant geography incorporated physiology, morphology and Darwinism into its explanatory structure. Schimper's work well exemplifies these new developments. Schimper was thoroughly acquainted with Grisebach's work and made frequent references to Die Vegetation der Erde:-

> "The connexion between the forms of plants and the external conditions at different points on the earth's surface forms the subject-matter of oecological plant-geography, which has only recently become a prominent subject of interest, although it found a place in earlier works, especially in Grisebach's valuable "Vegetation der Erde" ... "[258]

Schimper's classification of the world's vegetation was very similar to Grisebach's. But Schimper, unlike Grisebach, was strongly Darwinian and interpreted the facts of plant distribution and morphology accordingly. As Cittadino has recently put it:-

> "From the viewpoint of plant geography, Schimper's work falls within the tradition of Grisebach but ... Schimper was concerned not only with the nature but also with the origin of adaptation."[259]

Likewise it was Schimper's programmatic intention to incorporate new physiological interpretations into his analysis of the correlation between vegetation and environment:-

> "The oecology of plant-distribution will succeed in opening out new paths on condition only that it leans closely on experimental physiology, for it presupposes an accurate knowledge of the condition of the life of plants which experiment alone can bestow."[260]

It is, thus, impossible to claim that Schimper's "oecological plant-geography" was simply a direct continuation of Humboldtian plant geography. But the content of Plant Geography upon a Physiological Basis was nevertheless, as we have seen, strongly conditioned by the prior existence of the Humboldtian tradition of inquiry.

We can see a similar relationship between new and old elements in the work of Eugen Warming, Professor of Botany at the University of Copenhagen.[261] In terms reminiscent of Franz Meyen, Warming distinguished his activity from floristic plant geography which:-

> " ... is concerned with -
>
> 1. The compilation of a "Flora", that is, a list of species growing within a larger or smaller area. Such lists form the essential basis of the subject.
>
> 2. The division of the earth's surface into natural floristic tracts ... according to their affinities ...
>
> Oecological plant-geography has entirely different ends in view:-
>
> It teaches us how plants or plant-communities adjust their forms and modes of behaviour to actually operating factors ... Oecology seeks -
>
> 1. To find out which species are commonly associated together ...
>
> 2. To sketch the physiognomy of the vegetation and the landscape ...
>
> 3. To answer the questions -
> Why each species has its own special habit and habitat,
> Why the species congregate to form definite communities,
> Why these have a characteristic physiognomy.
>
> 4. To investigate the problems concerning the economy of plants ... We thus come to the consideration of the growth-forms of plants."[262]

There is much here we have seen before - the concern with physiognomy and "definite communities" for example.[263] Apart from morphology, the major new element in Warming was the concern with evolutionary adaptation. But this new preoccupation was to exist within a familiar framework of vegetational research. Warming continued to classify vegetation into natural units, according to physiognomy. He elaborated a new system of classifying the growth-form - contributing to a research practice he traced from Humboldt through Grisebach to his own contemporary Oscar Drude.[264] He was concerned with relatively smaller, more localised pieces of vegetation than Schimper's climatic formations. But he was concerned also to correlate these with the physical environment and to understand the effect of the environment on the structure of the plant.

Tobey has recently argued that Warming's 'Darwinian' concept of a competitive struggle for survival separated him from the 'idealistic' tradition of Humboldt and Drude.[265] Tobey is wrong on two counts. Warming was certainly interested in evolution and the origin of adaptation. But he was not a Darwinian in the sense that he favoured the mechanism of natural selection. In fact, like many early ecologists, he was famous for his Neo-Lamarckianism.[266] Secondly, Warming was, as we have seen, quite unequivocal about the existence of 'definite' plant communities - one of the features Tobey identifies as 'idealist' in the Humboldtian tradition. Of course the Humboldtian research tradition was sufficiently flexible to allow such communities to be conceived of in a variety of different ways. But there is no evidence in Warming's work that he did not allow the existence of, to use Tobey's terminology, "functioning communit[ies] of ontological status".[267]

Warming could in fact be said to be nearer to Humboldt's ideas on physiognomy and the relation between vegetation and climate than many of his contemporaries. This is because Warming argued that species and physiognomic growth forms "stand in perfect harmony (epharmony) with the environment" and that "plants possess a peculiar inherent ... faculty by the exercise of which they directly adapt themselves" to their surroundings.[268] In other words, vegetation is the creation and the expression of the environment - a very Humboldtian idea.

The bibliography of Oecology of Plants reads like a roll-call of Humboldtians - Hult, Schouw, Meyen - back to Humboldt himself. And, most significantly, Warming, like Schimper, cited no author who wrote prior to Humboldt. No eighteenth-century botanist, no-one who worked within the old episteme, is cited. The Essai sur la Géographie de Plantes was the principal starting point, one might say the fountainhead, for Warming's and Schimper's research enterprise - an enterprise which was unequivocally ecology.

The last member of the trio named at the start of this section - Oscar Drude - is the one with the most direct links to Humboldt. Drude was, from 1871 to 1873, research assistant to August Grisebach at Göttingen.[269] Drude regarded himself as continuing Grisebach's work in plant geography.[270] He put a strong emphasis on the unitary integrity of the regional formation - the character of which was determined by the regional climate. The formations were, however, internally heterogeneous due to the effect of topography upon the vegetation. Drude developed further Grisebach's system of growth-forms but he characterised the formation more floristically than Grisebach had done.[271] Smaller local units, characterised by dominant species within the large physiognomic formations, were termed '<u>Bestände</u>'.[272]

Drude's work provides us with another link between Humboldtian plant geography and twentieth-century ecology because his <u>Deutschlands Pflanzengeographie</u> was taken up by Pound and Clements as the model for their early investigations into the phytogeography of Nebraska.[273] This work founded one of the most important schools of plant ecology in America.[274]

<u>Conclusions</u>

This chapter began by investigating the reasons why vegetation first became an object of scientific study. [This part of the argument has already been summed-up in the section entitled "Why a science of vegetation"] The latter part of the chapter has gone on to trace the development of the study of vegetation, as a distinctive form of botanical inquiry, from Humboldt to the end of the nineteenth century.

It is clear, however, that we must be on our guard against the danger of identifying Humboldt too closely with later practice. As I hope this chapter has made clear, Humboldt's complex of interests does not fit neatly within twentieth-century disciplinary boundaries. Humboldtian science corresponds to none of our modern scientific subjects or specialties.[275] It would be downright misleading to refer to Humboldt as an ecologist; one calls him a plant geographer at some large risk of anachronistic identification.

He was, one might say, primarily a 'Kosmos-ologist'; or to use his own term, a student of "la physique générale" - a cognitive framework within which plant geography had a key role. However plant geography was, to Humboldt, a most important synthetic subject - a study indeed of Kosmos-ological significance. It was thus quite different in scope and importance from what we now know as plant geography or, even, plant ecology.

However I would argue that it remains legitimate to trace within Humboldt's work the roots of concepts later employed by botanists, ecologists and ecological plant geographers within the cognitive frameworks of these specific disciplines. For not all the Humboldtians could be as Kosmos-ological or as polymathic as the great man himself. Other men - Humboldtians in that they were associated with Humboldt, shared something of his cognitive framework, followed the exemplar contained in his scientific writings, used instruments in the manner he recommended, studied some of the objects he studied, and so forth - were to employ the resources presented to them by his work in more specialised, more circumscribed contexts - contexts which more closely resemble our present disciplinary divisions. Grisebach and Hult, for example, were primarily botanists - they were not necessarily students of all the ramifications of "la physique générale". But to show that scientists after Humboldt were more restricted in their range of interests than Humboldt was, is not to disprove that they were practitioners of Humboldtian science as they saw it applicable within their own subjects.

One must remember that in Humboldt's own lifetime, German science was in the process of dividing into professional specialties, and the reformed system of German university education was producing graduates trained specifically within those specialties.[276] Thus the Humboldtian tradition necessarily extended into an age of greater specialisation in natural science - extended indeed to the birth of ecology as a named and identifiable specialism in its own right.

Of what use to historiography is this idea of a tradition of Humboldtian plant geography? Firstly, it illustrates the heuristic value of the Foucaultian notion of episteme. It extends and supports his analysis of the difference between the cognitive frameworks of discourse of the eighteenth and nineteenth centuries. An understanding of Humboldt's attitude to vegetation clarifies the character of the new nineteenth-century episteme and helps us to follow the changing nature of the relationship between Man and his natural environment.

Secondly, it provides support for Susan Cannon's argument that the identification of a distinctive Humboldtian form of scientific inquiry is a powerful historiographical tool and an aid to our understanding of the science of the nineteenth century.[277] Furthermore, my account of Humboldtian plant geography puts flesh on the bones of Cannon's thesis - by extending the search for Humboldtian science into areas which she did not investigate. Cannon, writing Anglo-American history, did not look for Humboldtians in Humboldt's homeland nor in the country he adopted as his home in the middle years of his life - France. Cannon's attention was thus concentrated too narrowly to deal adequately with the complete phenomenon of Humboldtian science. It has been a serious flaw in our understanding of Humboldt's legacy that historians have, in this context, so far largely ignored those scientists who read Humboldt not in translation, but in the languages in which his work was originally published, and who talked and corresponded with Humboldt in those languages.

The search for Humboldtian science has, so far, been peripheral - and not only geographically. It has also ignored the obvious in the selection of disciplines within which Humboldt's legacy has been sought. The major omission here has been botany. Yet the importance of botany to Humboldt and of Humboldt to botany are both well known.[278] Of the thirty volumes of Voyage aux régions équinoxiales du Nouveau Continent - Humboldt's record of his scientific exploration in South America - sixteen, that is to say more than half, were concerned with plants or their geographical distribution.[279] Botany is thus the logical starting point for any study of how the exemplars offered by Humboldt were articulated in an era when disciplinary boundaries were becoming more defined.

Thirdly, a characterisation of Humboldian plant geography helps us to understand why vegetation became an object of scientific study. And it sheds light on why vegetation was held to be divided into natural units, thus illuminating the origin of one of the principal study objects of plant ecology - the vegetation type. Furthermore, it should alert historians of biogeography to the possibility, so far unexplored, that the distribution of species was not the only form of biogeographical activity undertaken in the nineteenth century.

Fourthly, an acceptance of the existence of Humboldtian plant geography and a recognition of its particular concern with vegetation would resolve doubts which at present exist as to what might be called the prehistory of ecology. It has often been said that plant ecology sprung quite suddenly into existence at the end of the nineteenth century - fathered by the inspiration of Warming, Schimper and Drude's great texts.[280] The story is often found in the reminiscences of British and American ecologists that one or other of these books so excited interest that the reader set out to put the precepts of the continental authors into practice in their own countries.[281] No doubt these accounts are true, to a large extent. Such stories have, however, become received as part of the official history of ecology - and received as the explanation of the origin of the subject, not simply its transmission to Britain or America. As Worster put it:-

> "Their [Drude, Schimper, Warming] work during the 1890s transformed Oecologie from just another neologism to a functioning science with its own peculiar hold on reality."[282]

Goodland dubbed Warming "the founder of plant ecology".[283]

However, Godwin has pointed out the obvious over-simplification inherent in this account of the origin of ecology.[284] He traced the influential Zurich-Montpelier school back beyond 1890 and showed that one of its founders, Carl Schröter, was well set on his ecological research independent of the work of Warming and Schimper. Likewise, Sernander had already started applying quantitative methods to the study of vegetation in the mid-1880s. So the two great continental schools of vegetation science were founded before Warming and Schimper published. The existence of plant ecology, or something like it, must be the explanation for Warming and Schimper, and not vice-versa. Indeed, it only requires the briefest look at the Lehrbuch der Ökologischen Pflanzengeographie or the Pflanzengeographie auf physiologischer Grundlage - at their size, scope or bibliographic comprehension - to see that these great texts could not have been produced by men who were simply the rude forefathers of a nascent scientific specialism. It is clear that these texts themselves represent the culmination of many years of inquiry, of a long tradition of research into vegetation. But what sort of tradition did ecology spring from? I would contend that I have discerned, extending from Humboldt to Drude, Schimper and Warming, that tradition of research. As a research programme it was certainly flexible; it diverged into several schools; it incorporated new elements - but it is discernible throughout the nineteenth century neverthless. And I would contend that it was largely from this pre-existing tradition that plant ecology developed at the end of the century. Schröter, Sernander and Drude were all third generation students of Humboldtian plant geography.

This novel perspective allows us to see the development of later views of vegetation and the plant association not as isolated or independent events, but as part of a continuing story of cognitive change and development.

CHAPTER TWO

DIVERGENT CLASSIFICATIONS - THE CLEMENTSIAN AND SIGMATIST CONCEPTIONS OF THE PLANT ASSOCIATION

Introduction

The importance of the idea of a supra-individual unit of vegetation of "orderly structure and correct composition"[1] was not to diminish in the twentieth century. From Schouw until the 1960s, there was an almost complete consensus among plant ecologists of all nations that vegetation was made up of natural units, recognisable, at least in principle, as discrete entities with real boundaries. These units were generally regarded as part of the structure of nature - not just the product of particular methods of investigating vegetation or the product of processes of classification. The term 'association' expressed this belief that 'essentially' the same groups of plants were to be found growing together in different locations.[2] The associations were taken to be the proper basis for ecological study.

The pre-eminent British ecologist Arthur George Tansley put the matter succinctly:-

> "But if we admit, as everyone who has worked at the subject does admit, that vegetation forms natural units which have an individuality of their own and that these units owe their existence to the interaction of individual plants of different species with their environment then it becomes clear that a mere study of the distribution of species as species cannot form the basis of the science of vegetation. We have instead to focus our attention on the vegetation units themselves."[3]

American and European ecologists concurred almost to a man. The following quotation is taken from a major American ecological text-book:-

> "Vegetation responds [to climatic factors] by its distribution into groups, each of which is in close equilibrium with its particular climatic complex ... The plant formation is the major unit of vegetation. It is a fully

developed or climax community of a natural area in which the essential climatic relations are similar or identical. Each formation is a complex and definite organic entity with a characteristic development and structure."[4]

H.S. Conard's views were equally representative:-

"The association of individuals and species is much more than a chance meeting. It is part of the order of nature ... Associations of plants on land are definable entities, susceptible of naming and classifying.[5]

Carl Schröter and Charles Flahault "the fathers of the Zurich-Montpelier school"[6] successfully proposed the following definition to the nomenclature committee of the International Botanical Congress of 1910.

"An association is a plant community of definite floristic composition, presenting a uniform physiognomy and growing in uniform habitat conditions. The association is the fundamental unit of synecology."[7]

So fully accepted was the theory that there were natural kinds of vegetation that it did not even have a name until 1956 - when R.H. Whittaker, an American ecologist and one of the first men to achieve real influence in dissent from this theory, dubbed it the 'association-unit' or 'community-unit' theory.[8] Like the cell theory and the species theory, the community-unit theory was a conception of the inherent structure and organisation of the phenomena with which scientists dealt. F.E. Clements expressed it most succinctly of all:-

"The final task of phytogeography is the division of the earth's vegetation into natural areas."[9]

In the twentieth century, the attempt to describe the plant communities of the world and to understand why each occurred where it did became a research enterprise of enormous size and scope. The literature on the study of natural communities runs to uncounted thousands of papers, in all the languages in which scientific papers are published.

This scientific enterprise and its sub-divisions have been given many different names in different countries and contexts - geobotany, ecological plant geography, plant ecology, phytosociology, and many more. These names often map out real distinctions of practice or social divisions between practitioners, but to elucidate these distinctions fully here would deflect me from the task presently in hand. With all due apologies to those practitioners who may feel that such a cavalier procedure masks vital distinctions between different research programmes, I intend to cut this Gordian knot of labelling and nomenclature. I shall refer, for the remainder of this thesis, to the whole of the scientific study of vegetation, wherever and however done, as either 'vegetation science' or 'plant ecology'. I shall take these terms to be virtually synonymous and one will be used rather than the other simply for reasons of variety. Vegetation science therefore, in the present usage, encompasses both what the Europeans call 'phytosociology' and what the Americans call 'plant ecology'.[10]

In all forms of vegetation science, classification has been centrally important. In describing and explaining the phenomena of vegetation it is necessary to subdivide one's subject-matter in some way. This is, of course, a characteristic that ecology shares with other scientific disciplines.[11] But, in ecology, the importance of classification has been especially emphasised by the central position accorded to the methodology of classification. Not only have ecologists been concerned with identifying associations from within the remarkedly complex and varied mantle of the Earth's vegetation, they have often attempted to relate the associations to each other in categories of higher syntaxonomic rank. Many ecologists have gone so far as to regard the construction of a comprehensive system of classification as the primary aim of vegetational research, of great interest in itself and providing the essential framework without which other ecological research is unlikely to be well-directed or profitable.[12]

Broad agreement over the importance of classification has led to intense research activity but no universal consensus has emerged as to which is the best way to classify vegetation. Despite the fact that a fundamental unit to be used as the basis for a synthetic classification (as the species is used in the taxonomy of individual plants) has been generally agreed to exist, and has been actively sought, for more than a hundred and fifty years, there has never been agreement about the nature and extent of the putative unit or the basis on which it should be described. According to some schools, particularly in Europe, the vegetation unit (the association) was a small-scale, homogeneous community, whereas to most Americans, the association was a large-scale unit including within itself great variation. Thus whereas H.S. Conard, using methods derived for European phytosociology, described 71 associations in central Long Island, Clements recognised only three in the entire eastern deciduous forest of the United States.[13] No aspect of ecological science has been the subject of more discussion and argument nor has had a more central role in the differentiation of ecology into schools of differing research practice than this debate over which is the best way to classify vegetation.[14]

The last sentence is a paraphrase of the opening lines of R.H. Whittaker's major review of the methods used to classify vegetation, which was published in 1962.[15] It ran to 239 pages and the bibliography, described by its author as "reasonably comprehensive", contained more than 1700 titles. It outlined the standpoints of seven major traditions of classificatory practice, each of these internally divided into disputing sub-schools.[16] Since 1962, thousands more articles classifying vegetation have been published in all the major languages. If some of the issues seem less controversial now than they did then, it is because the debate has flowed in new directions. Very little has been resolved to the satisfaction of even a majority of workers in the field. Vegetation science is still as divided into schools as it ever was.

These apparently endemic differences between the schools have created some problems for commentators on classification within the ecological profession. If, the problem runs, most classifications are claimed by their perpetuators to be descriptions of the reality of vegetation, not conventional or instrumental representations, and ecologists are generally reasonable men (as ecologists must believe is the case), then why do the different schools classify in such diverse and different ways? Perhaps a certain amount of divergence may be ascribed directly to error, or mere factiousness, or personal idiosyncracy or rampant subjectivity on behalf of the investigators. But only a certain amount - if ecology itself is not to be unnecessarily discredited. It is obvious that several radically different classifications have been sufficiently successful in describing vegetation to allow these descriptions and the methods of arriving at them to have been transmitted to generations of students, to have supported lengthy research programmes, and to have found very fruitful practical applications.[17]

This successful pluralism has led to the claim that the explanation for the differences between the schools is to be found in systematic differences between the characteristics of the world's vegetational regions. For example, the lower biological productivity and species-richness of the vegetation of Scandinavia, when compared with that of Southern Europe, could explain the difference between the Uppsala and Zurich-Montpelier systems - each accurately reflecting the vegetational reality of its own area of study.[18]

This type of explanation, which neatly harmonises the discipline's commitment to realism with its observed lack of unity in practice, has been called the 'ecology of ecological traditions', or the 'ecology of ecologists'.[19] The present chapter will examine this explanatory thesis critically. It will also consider, as an alternative explanation, whether the different vegetational classifications may best be thought of as conventional, and if the explanation for their divergences is to be found in the differing social contexts of the research groups who employ them.[20]

To this end detailed consideration will be given to two of the historically most important schools - the one derived from the work and teaching of J. Braun-Blanquet, which is a variant of the Zurich-Montpelier or Southern European school, and the system of the American ecologist, F.E. Clements. For the sake of simplicity, each school will be treated as being more internally homogeneous than it actually was - or, in the case of the former example, actually is, since students of Braun-Blanquet are still active. This simplification is more of a distortion in the case of the European example than it is in the case of the American one. Braun-Blanquet's approach has undergone considerable modification, especially when employed far from its European homeland.[21] For the purposes of this chapter, the Braun-Blanquet system will be described more or less as it was formulated by the man himself, and by his immediate followers and associates.

The structure of this chapter is complicated and the reader must be prepared for quite sudden changes of scene - as aspects of the American system or its context are compared with their European equivalents or vice-versa. Such movements may sometimes be confusing, but I hope the reader will bear with me. The advantage such interweaving comparisons possesses over a more straightforward presentation is that the shaping of each school by its contingent social circumstance may be more readily displayed. I hope that the divergence between the American and the European systems of vegetation science illustrates that what we witness in the history of each school is not the rectilinear march of scientific knowledge toward greater correspondence with natural reality, but a process whereby knowledge production is shaped by the particular culture which sustains it. Comparison enables the individuality of each set of social circumstances to be more readily apprehended.

The chapter begins with a short account of the development and differentiation of each school from the tradition of Humboldtian plant geography. The story is taken up just where the previous chapter left off - at the birth of a 'self-conscious' ecology.[22] The nature of the vegetation units employed in America and in Southern Europe will be outlined and contrasted. I will then consider the 'ecology of ecologists' theory as a possible explanation for these differences. Having found it wanting, I will examine the adoption of a taxonomic exemplar by Braun-Blanquet and his colleagues. This will be interpreted in the light of their involvement in the professional conflicts and competitions of European botany in the early twentieth century and in the light of the skills which they acquired in the course of their botanical training. Clements's adoption of a different model subject - physiology - will be interpreted in the context of the different social circumstances of American botany, particularly in the Western and Mid-Western States and in the Land-Grant Colleges. I will consider in detail the effects of a necessary commitment to applicable science upon the theory, rhetoric and professional aspirations of the Clementsian ecologists.

Braun-Blanquet and Sigmatism

Josias Braun was born in Coire, Switzerland in 1884.[23] His botanical training was under the guidance of two famous botanists, Carl Schröter of Zurich and Charles Flahault of Montpelier. It was under the supervision of Flahault that Braun did his doctoral thesis in 1915 on the phytogeography of the Southern Cévennes. Also in 1915, after his marriage, he added his wife's name to his own and thereafter published as Braun-Blanquet. From 1916, he was Privatdozent at the Ecole Polytechnique Fédérale in Zurich, where he worked under Schröter and where he collaborated with another famous student of Schröter's, Eduard Rübel.

By the time Braun-Blanquet took up graduate studies, the vegetation science done at Zurich and Montpelier was already recognised as the product of a definite school. The early work of Heer, Lecoq, Christ, Kerner and Bonnier (all botanists in the Humboldtian tradition) on the rich and varied vegetation of the Alps and Southern Europe had been further developed in the twentieth century by Schröter, a student of Heer, and Flahault, a student of Bonnier, and by their students in turn, such as Brockmann-Jerosch, Rübel and Pavillard.[24]

These botanists had studied vegetation in relation to the effect of climate and other environmental factors on its form. They had used a wide assortment of vegetational features to characterise the units of vegetation on which their work was based, employing both physiognomic and floristic criteria in their classificatory procedures. Units determined by floristic composition were often regarded as being hierarchically related to larger units determined by physiognomic structure. For example, several sorts of deciduous wood each characterised by the presence of different species of tree or shrub might all be grouped under a larger unit of forest-type characterised by the growth-form of the deciduous tree.[25]

The distinctive difference between Braun-Blanquet's approach and that of his Southern European predecessors may be seen in the work he did while a graduate student at Montpelier.[26] His choice of classificatory criteria was narrower and their use more formalised. Physiognomy had no part to play in his systematic classification of vegetation. The basis of classification was to be floristic composition - and nothing else. Furthermore, floristic criteria were to be interpreted strictly. Determination of vegetation-types was to be by 'characteristic' species, revealed by detailed floristic analysis, rather than simply by dominant species, as had been used by, for example, Flahault.[27]

Braun-Blanquet's work was so influential as to make his name virtually synonymous with the purely floristic approach to vegetation science.[28] However it is important to note that similarly floristic methods were advocated by Brockmann-Jerosch in 1907 and by Gradmann in 1909.[29] These works, together with Braun-Blanquet's, collectively established the distinctive Zurich-Montpelier practices of identifying 'character' species from within floristic associations and of compiling sample lists for collation into community tables.

Pavillard, a professor at Montpelier, also early adopted a floristic approach to plant community. In the nineteen-twenties the floristic programme continued to develop in a series of papers by Braun-Blanquet and Pavillard, either singly or together.[30] In 1929, Braun-Blanquet moved to Montpelier. A unified and organised system of floristic phytosociology was presented to the world with his publication in 1928 of _Pflanzensoziologie_.[31] Whittaker has described this text as "one of the two most influential books in the classification of communities, influencing many phytosociologists as profoundly as Warming (1909) has influenced English-speaking ecologists."[32]

The independence of Braun-Blanquet's research programme was institutionalised in 1930 when he was appointed director of the newly-established _Station Internationale de Géobotanique Méditerranéene et Alpine_ at Montpelier.[33] Sigma, as the station was often called, has served ever since as the headquarters and training centre for the school of Braun-Blanquet. Braun-Blanquet's approach is itself often referred to as Sigmatism. The many younger scientists and the many hundreds of research publications which Sigma has produced evidence the impact of Braun-Blanquet's system and its sustained development and articulation.[34]

F.E. Clements and the Plant Formation

The school of Braun-Blanquet is still active. There are still botanists who would describe themselves as Sigmatists. The system of his American rival, F.E. Clements, is defunct to the extent that no ecologist (to my knowledge) still refers to himself as a Clementsian. But F.E. Clements's work was immensely influential on American and English-speaking ecology for many years, and it has been claimed that some of his conceptions have survived the unpopularity of his system by taking on new names in more modern ecological theory.[35]

F.E. Clements was born in Lincoln, Nebraska in 1874.[36] After graduating from the University of Nebraska in 1894, he became a member of an industrious and productive group of young botanists which had gathered around the head of Nebraska's Botany Department, Charles E. Bessey.[37] Bessey was among the foremost of those botanists who were working toward the introduction of the 'New Botany' into the United States.[38] The New Botany had originated in Germany. What was new about it was its orientation toward plant physiology and morphology, toward experiment and laboratory methods.[39] Bessey saw the experimental emphasis and the evident prestige of the New Botany as capable of improving the status of Botany within American Science. He was one of the first American botanists to teach students in the laboratory, and his graduate students organised themselves into a Botanical Seminar in conscious (if inaccurate) imitation of the forms of German graduate education.[40]

In 1898, Clements, in collaboration with Roscoe Pound (also a member of the Botanical Seminar and a student of Bessey), produced The Phytogeography of Nebraska.[41] This text was modelled explicitly upon Oscar Drude's newly published Deutschlands Pflanzengeographie, which both authors greatly admired.[42] This was followed in 1904 by the first presentation of Clements's comprehensive system of vegetation science "The development and structure of vegetation" and in 1905 by the textbook Research Methods in Ecology.[43] The latter dealt with, among other things, the practical analysis of vegetation by the quadrat and transect techniques, newly devised by Pound and Clements, and with the use of environmetric recording instruments in the field.[44] The research programme contained in these two publications was developed in an impressive series of books and articles culminating in 1916 with the publication of Plant Succession - an analysis of the development of vegetation.[45] This book has been regarded as the paradigmatic presentation of the Clementsian system.[46]

In 1907, Clements became Professor and Head of Department at the University of Minnesota. He held this position until 1917, when he joined the Carnegie Institution. He remained with the Ecology Section of the Carnegie until his retirement in 1941. He died in 1945.

The primary unit of the Clementsian system was termed the 'formation' and was large in area, encompassing great variation, and including within itself several regional 'associations'. Each formation was said to be distinguishable by a combination of physiognomic, floristic and habitat - that is physical - factors. The formation was defined as the typical or 'climax' community of an area over which the climate was 'effectively uniform'. Theoretically, uniformity of habitat had primacy in the determination of the extent of any vegetation unit but, in fact, 'efficient differences' in the habitat were recognised only by their producing differences in the plant cover. Since, by definition, the true dominants of any one formation had to be all of the same life-form, in order that the formation present a unified response to the uniform climate, Clements's formations were in effect physiognomic units.[47]

Examples of vegetational areas designated by Clements as formations were the deciduous forest of the eastern United States, and the prairie-plains grassland of the Central West. All in all, only twenty formations were needed to classify the vegetation of the entire United States in 1916, and further work had reduced this to 14 by 1938.[48] There was, of course, considerable subdivision within each major formation. The prairie-plains grassland formation was divided into 8 important associations - examples of which were true prairie, tall-grass prairie, short-grass prairie, desert plains, and so on.[49]

As is implied by its being said to occupy a definite area, the Clementsian formation was considered to be a concrete entity.[50] This was one of the most distinctive features of Clements's system. To Braun-Blanquet, the association was a real but abstract category of which the stands of vegetation observed on the ground were the concrete representatives.[51] According to Clements, the stands did not bear this relation to the formation. They were rather the component parts of a larger structure.[52]

In Braun-Blanquet's work, two basic analogies are made. One is between the stands of vegetation observed in the field and individual biological organisms. The other is between the association and the taxonomic species into which both the former are classified.[53] Clements, however, regards the formation as itself analogous to the individual organism.[54] The stands are thus to be considered as parts of the structure of the formation as organism - presumably to be thought of as the equivalent of the tissues or cells of an individual, although Clements never specifies a precise analogy.

Braun-Blanquet solved the problem posed by there obviously being more than one kind of vegetation in any given area by allocating the different types to different associations. To Clements, however, whatever vegetation fell within an area of effectively uniform climate was, of necessity, all part of the formation characteristic of, and controlled by, that climate.[55] Stands of vegetation lying within the area of a formation but physiognomically distinct from that deemed typical of the formation were said by Clements to be connected <u>developmentally</u> with the climax vegetation. They are immature forms of parts of the 'super-organism'. The processes of vegetation succession, soil maturation and geomorphological base-levelling would eventually, if the climate were to remain constant, allow all the vegetation growing within the geographical limits of the formation to develop into the highest form of vegetation possible under the given climate. For example, the highest form of vegetation possible in the Tropics would be Tropical Rain-forest, in Northern Canada coniferous forest, further North still, tundra, and so on. This was known as the 'monoclimax' theory - only a single vegetation type was true climax within any given climate.[56]

In the first three decades of the twentieth century, investigations into the processes of plant succession and vegetational change were, for reasons I will explain in the next chapter, being undertaken by virtually every American plant ecologist. In Europe, investigations of vegetational change were never of such central importance. The Americans became fond of contrasting their 'dynamic' approach with the allegedly 'static' conception of vegetation employed by the European phytosociologists.[57] The organismic development theory of the climatic climax was a peculiarly Clementsian expression of this American interest in vegetational change.

One might characterise the difference between the Clementsian and Sigmatist viewpoints concisely in the following manner. The Braun-Blanquet system involved the identification in the field of small-scale stands of characteristic and actually uniform (that is to say apparently or virtually uniform) floristic composition. These stands were then classified into abstract taxons, the associations, in a manner analogous to that used by taxonomists to classify individual specimens into species or genera. The Clementsian system, on the other hand, depended upon the identification in the field of large concrete units of characteristically uniform (or potentially uniform) physiognomy. By definition all the dominants of a particular climax formation had to have the same growth form - since the dominant growth form was a direct expression of the climate.[58] Areas of vegetation of physiognomy different from that to be expected within any given climate were regarded as merely stages toward the climax form. Succession would displace them and usher in a vegetation with the climatic climax life-form. Thus, the existence of hemlock, Tsuga canadensis (a coniferous tree) in the deciduous forest was intepreted by Clements as evidence of a previous southern extension of the boreal forest. The hemlock was a relict, temporarily surviving outside its 'proper climax position'.[59]

The ecology of ecologists

Overall, the two systems of vegetation science embodied quite different views as to the nature of vegetation. How can these differences between two of the most successful schools of plant ecology be explained? Bearing in mind the 'ecology of ecologists' explanation referred to above, to what extent were these differences due to the distinctive characteristics of the vegetation which each school studied?

It is certainly true that the large expanses of the Prairies and the Plains confronted turn-of-the-century American ecologists with a vegetational aspect very different from that to be encountered in Southern Europe at the same time. Much of the American West and Mid-West, although already greatly disturbed by Man, had been pristine within living memory and the original character of the vegetation was often still quite clearly discernible.[60] The great grasslands were, above all, startlingly homogeneous over huge tracts of land. This was a feature of the landscape which all its early observers commented upon.[61] On the other hand, European vegetation was, generally speaking, broken up into quite small patches, due to agriculture and, especially in the Alps, where Schröter, Heer and others had done their pioneer studies, to a rugged and varied topography. Also European vegetation had obviously been quite radically modified by Man in the course of hundreds of years of exploitation. The large tracts of virgin climax vegetation had long since vanished.

But any attempt at building such 'ecological' observations into a comprehensive explanation of the differences between the Zurich-Montpelier and the Clementsian schools immediately encounters serious problems. It is not simply in matters of size that the differences lie - the respective ecological units are different in character. The Clementsian unit is a physiognomic one bearing, in principle, a one-to-one relationship to an area of uniform climate. The unit of Braun-Blanquet is a floristic one, the distinctive floristic composition of each unit being a response to the totality of environmental influences.[62] It might perhaps be argued that an observer experienced in the study of large expanses of relatively homogeneous vegetation - such as occurred over large parts of the American West - would tend to couch his ecological explanations in terms of unifying large-scale environmental factors such as the regional climate. On the other hand, experience of the relatively small and relatively isolated stands of European vegetation might lead the observer to think in terms of a smaller fundamental unit of vegetation. The absence of intermediary types might render the floristic individuality of individual stands more apparent. But it is difficult to see how such an argument could explain why the Clementsian unit was held to be concrete and organismic and the Sigma unit to be abstract.

Furthermore, to have any explanatory force, such 'ecological' arguments would have to be of some general application. However, several damaging counter-instances exist. For example, the vegetation of the British Isles is every bit as anthropogenic and broken-up into small patches as that of continental Europe. Floristically, the British and European vegetations are very similar. Yet neither the Braun-Blanquet association nor any other small floristic unit of the Continental type has ever had much popularity in Britain.[63] British ecology has always been much closer in character to its American counterpart than it ever was to European phytosociology, despite the vegetation of the British Isles being quite different from that of the Mid-West, the formative centre of American ecology.[64] Likewise, American ecology has not often had much in common with Russian ecology, despite the fact that the scientists of both countries dealt, in some situations at least, with similarly expansive and comparatively undisturbed vegetation.[65]

Therefore we may conclude that the nature of vegetation does not fully determine the character of the units into which any given piece of vegetation is classified. This conclusion, however, does not imply that the nature of vegetation is irrelevant to the manner in which vegetation is conceptualised by ecologists. Many of the differences between the Zurich-Montpelier and Uppsala schools, or between European and American vegetation science, undoubtedly do express differences in vegetational reality. What the deficiency of the 'ecology of ecologists' explanation does entail, however, is that we must look at factors other than the input from the natural world, if we are to have a complete explanation of the differences between the Clementsian and the Sigma schools. As in the previous case-study, we must look at the cultural contexts and what one might call the purposes, the relations to social and cognitive interests, of the respective research programmes. This was acknowledged by Whittaker:-

> "Classifications are affected also by objectives of research, as these are influenced in part by ecological conditions, in part by possibilities for practical applications in relation to these ecological conditions, and in part by more purely cultural influences on scientific outlook and objectives ... History and present problems of classification are to be understood through the ecological, cultural, and personal influences affecting them ...Ecological schools too, have their "ecology" but may also have distinctive characters not clearly determined by their "ecology"."[66]

Braun-Blanquet and the model of taxonomy

Consideration of the different analogies employed by the two schools is instructive as to where our search for a fuller explanation ought to begin. Firstly, the analogy of the association to the species was prominent in all of Braun-Blanquet's writings. Braun-Blanquet's phytosociological practice was firmly based upon the model of plant taxonomy. Indeed Braun-Blanquet erected the entire edifice of his phytosociological classification so as to make it as similar in structure as possible to that of the floristic study of individual plants:-

> "[Plant sociology's] definite objective, however remote its accomplishment, is to catalogue and describe the plant communities of the earth, to discover their causal explanation, to study their development and geographic distribution, and to arrange them according to a natural system of classification."[67]

Under the Braun-Blanquet system, floristic evidence was the only sort allowed in the characterisations of associations. The field practice of the phytosociologist must, therefore, be based upon the species units as determined by the taxonomist:-

> "Species ... are groups of individuals with uniform inheritance and have been for many years the object of

careful investigation. In the species are embodied certain definite adjustments to and demands upon the environment. Hence the species have come to be regarded as conspicuous indicators of certain conditions of life ... Precise recognition of species is therefore the first and indispensable requirement for the phytosociologist."[68]

The flora of a study area must therefore have been worked out by taxonomists before phytosociological research can begin. Phytosociology, thus, according to Braun-Blanquet, must be both dependent upon, and consciously imitative of, the science of taxonomy:-

" ... since all phytosociological classification rests upon a floristic foundation, it is exactly in this classification that systematic botany is of the highest service."[69]

Braun-Blanquet contrasted the well-organised state of the science of floristics with the comparatively undeveloped condition of research into physiognomy:-

"The countless individuals may be grouped in two distinct ways: under the concept of the taxonomic species or under the concept of growth forms or life forms. The Brussels Congress (1910) rightly decided in favour of the species as the fundamental unit for the plant community. The concept of 'life form' is indefinite, has not been adequately defined and cannot be considered as a sufficient basis for a science of vegetation."[70]

Likewise, Braun-Blanquet summarily dismissed the possibility of a classification based on the criterion of a uniform habitat as proposed by various British and American ecologists, including Clements:-

"A clear and unequivocal delimitation of habitats according to operative external factors appears quite unattainable ... On account of this difficulty, it is more and more necessary, in investigating the communities, to go directly to the vegetation itself. We then arrive at the point from which we should logically have started out: the natural groupings of plants. The natural unit of vegetation comes thus into the foreground of our study and, temporarily ignoring the habitat, we seek to recognize and define the floristic individuality of the communities."[71]

Phytosociology's utilisation of, and dependence upon, the species concept of orthodox taxonomy may be clearly seen in

Braun-Blanquet's description of how associations were to be identified in the field. Braun-Blanquet's procedure for the distinction and classification of units, as set out in Pflanzensoziologie, was wholly based on the floristic description of carefully chosen sample plots. In order fully to convey the role of taxonomic knowledge and skill in phytosociological practice, it is necessary to describe in more detail what this procedure entailed. This description will also highlight some other noteworthy features of Sigma's methodology.[72]

Firstly, it was considered most important that the vegetation of the chosen sampling site be uniform. However, the criteria by which uniformity was to be determined were not specified. Statistical testing for uniformity was not envisaged. Rather the uniformity of a prospective sample site was subjectively assessed by the phytosociologist, bearing in mind all the observable properties of the vegetation. The phytosociologist would seek to place his sample sites in areas which would provide samples illustrative of the characteristics of the vegetation of the study area as a whole, as determined by preliminary reconnaissance. The placing of sample plots was therefore an exercise of the fine discrimination, the 'Soziologischer Blick' which was held to be in the possession of the phytosociologist due to his long training and the depth of his experience of vegetation.[73]

Having chosen the stands he intended to study, the investigator would write a short description of their geographical location, altitude, aspect, major environmental features, and so on. Then all the species present in the stands were identified and listed. Ideally this list would be complete, including mosses, liverworts, fungi and lichens as well as vascular plants. To compile accurately and expeditiously such a catalogue of the sample area (which might be as large as four or even, in herbaceous vegetation, eight square metres) required great skill in the identification of plants. Specific determination was to be as exact as possible. Any specimens which could not be identified in the field were labelled and brought back to the laboratory where, if necessary, expert taxonomic advice would be sought. Every species in the list was given an index of cover-abundance (roughly speaking, how much of the surface-area of the stand it occupied) and sociability (whether it grew singly, in small groups, in large groups, in colonies or in pure populations).

In the laboratory, the species lists from all the sample plots of the study area were grouped in what were called 'association tables'. The aim was to put together lists which were similar in order to identify the number of different associations represented in the field data. According to Braun-Blanquet, decisions as to how many associations a given tabulation of species lists represented could only be made by consideration of the 'fidelity' of the various species. The theory was that certain plant species demonstrated strong selective preference for definite communities. Their presence in species lists might be used, diagnostically, in the characterisation of associations. Such species were called 'character-species'.

The determination of character-species was, in practice, extremely difficult. Few species were completely faithful to a single association. Also, the reasoning involved in identifying character-species was apparently circular.[74] Prior knowledge of the associations was necessary for the recognition of the character-species, and yet the character-species were to be used diagnostically to recognise the associations. In fact, no formal rules for the determination of character-species were given. Rather, the Sigmatists maintained that the process was something of a craft skill, developed through long experience, and best learned from an accomplished master.[75]

A character-species need not be at all an obviously important species within the community which it was said to be characteristic of, and faithful to. It was, for instance, not always a dominant species. It might be insignificant in terms of size, number of individuals or area covered within any sampled stand. Only an expert could discern its importance.

The end-product of the laboratory or 'synthetic' phase was the compilation of a characteristic species composition for each association. That is, the emphasis eventually shifted from a particular species with special diagnostic value, the character-species, to the association's entire species composition. The characteristic species composition typified the abstract plant association and might never be found in all its details in the field. Finally the units decided upon were checked in the field with new samples being taken. If the new samples did not correspond readily with the original tabulations, further associations might be described to accommodate them.

It can readily be seen that this whole process depended on the phytosociologist being skilled in the identification of plants and having the help of taxonomic experts. The phytosociology could only be sound if the underpinning taxonomy was itself well-founded. Braun-Blanquet argued that there was a strong symbiotic relationship between the two sciences. One of the strengths of phytosociology "dans le domaine des applications pratiques" was the help it could give to floristics:-

> "Le relevé des groupements végétaux exige une étude minutieusé de surfaces bien délimitées où rien ne doit passer imperçu. Cette façon de procéder amène la découverte de nombreuses espèces nouvelles pour la contrée étudiée, pour le pays tout entier, ou mêmes nouvelles pour la science. C'est en étudiant une garrique du Brachypodietum ramosi non loin de Montpelier ... qu'on a mis la main sur le fugace Sternbergia colchiciflora espèce nouvelle pour la flore française."[76]

Likewise, floristic study could aid phytosociology:-

> "Ponderous manuals and masses of plant lists tell us with increasing exactness about the occurrence and distribution of the species of our flora. These sources can also be made useful synchorologically by means of the fidelity of species. Oftentime an obscure floristic paper may enable us to predict the presence of a certain association. If several characteristic species occur together in one locality, the presence of the association in question may be predicted with a high degree of probability ... "[77]

The Sigma school's quasi-taxonomic approach was obvious in its grandest project - the attempt to systematise the plant communities of the world. The first fascicle of Prodome des Groupements Végétaux was published in 1933, and several other volumes have been produced since then.[78] In these works, associations were named in exact analogy to species, with Latin binomials, with rules of priority and synonomy, and with the author and date of the description appended to the name of the association. The environmental relations and distribution of each association were briefly described.

Sub-units were listed, having the same relation to the association as the variety has to the taxonomic species. The associations were arranged in a hierarchical system of alliances, orders and classes, modelled on the hierarchical arrangement of genera, families and orders in taxonomy. These higher categories were also given complete with citations and synonomy, and were defined, like the association, floristically by characteristic species. Physiognomic criteria were not employed at any level of the classification. As R.H. Whittaker put it, "In these works [the Prodomes] the ideas of Braun-Blanquet find their ultimate expression - treatment of natural communities in a form exactly paralleling manuals of floras".[79]

It has already been pointed out that the use of floristic data is not the only way to construct ecological classifications. Why was it adopted so rigorously by Braun-Blanquet and his followers? To answer this question we must look at the situation of contention and competition which obtained within the discipline of botany at this time.

Phytosociology and the New Botany

In the second half of the nineteenth century, botanists faced a choice of ways in which to direct their activities. The discipline had been swept by the New Botany with its novel emphasis upon physiology and morphology, upon experiment and laboratory methods.[80] The New Botanists proselytised for the application within botany of models of scientific practice ultimately derived from the physical sciences. This was originally a distinctively Germanic movement and was a product of the burgeoning of German science from the eighteen-forties onwards, due to professionalisation and new forms of scientific education.[81] However, experimental approaches to plant physiology also became popular in France and Britain, and, by a process of direct transfer from Germany, in the United States.[82]

On the other hand, many botanists were still practising, and were still training students in, more traditional activities - the collecting, identifying and classifying of the older natural history mode of botany, with its orientation toward the herbarium and toward observation in the field. Many of these traditionalists - for example, Babington, Professor of Botany at Cambridge - felt threatened by the aggressive New Botanists who, often quite explicitly, sought to relegate the expertise of the taxonomist to a subordinate status:-

> "It is rare now to find an Undergraduate or B.A. who knows, or cares to know, one plant from another ... I am one of those who consider this to be a sad state of things. I know much of what is called Botany is admirably taught among us; but it is not what is known as Botany outside the Universities, and does not lead to a practical knowledge of even the most common plants. It is really Vegetable Physiology, and ought to be so called. It is a very important subject, but it does not convey a knowledge of plants."[83]

Joseph Hooker, the Director of the Kew Herbarium and the doyen of British systematic botany, was also aware of the changes which were occurring in the study and teaching of botany:-

> " ... physiology, minute anatomy, and chemico-physiology, and into physico-physiology ... now form the staple of botanical teaching ... in this country. Botany is no longer a knowledge of plants, but how parts of plants "come about" and what they do! You begin with yeast, moulds, etc., and the higher you go the less you know the whole plant and the more of their "inwards". There is no question of the high scientific value and interest of all this, but the outcome of years of it may leave a man in utter ignorance of any plant bigger than the Torula or Mucor he began with."[84]

Hooker came to feel that the pendulum had swung too far towards the 'New Botany' and that the value of taxonomy and floristics was being unjustly ignored:-

> "There is a strong feeling apparent, that vegetable physiology and anatomy alone do not supply the wants of the public - and that some knowledge of plants in general, their uses, physiognomies and distribution, should be taught:- a knowledge of plants, in short as well as of their "innards" and movement."[85]

There was considerable professional conflict between the traditionalists and the New Botanists. F.O. Bower, one of the pioneers of the New Botany in Britain, had discontentedly read botany at Cambridge under Babington before going to Germany to study under the famous physiologist Julius von Sachs at Wurzburg, and the famous morphologist Anton de Bary at Strasbourg.[86] Bower complained bitterly about the dominance of the old floristic style of work at Cambridge:-

> "Thus while official botany at Cambridge has been splitting analytically the varieties of Rubus [one of Babington's special interests] the laboratory of Hofmeister in the Universities of Heidelberg and Tübingen, was glowing with a new synthetic flame; and a true comparative morphology had emerged."[87]

The New Botanists competed with the old guard for the relatively meagre resources available to the discipline as a whole:-

> "I [Bower] remembered about 1876 how I longed for a train of wagons to convey the Cambridge herbarium away to Kew, so as to vacate for the new botany the rooms that would have served its needs."[88]

Despite the conflict there was, as we have seen in the previous chapter in the work of Schimper, for instance, also scope for combining these two forms of botanical activity. A place could be made for the old skills within the context of the New Botany. From this perspective it is interesting to look at the work of Gaston Bonnier, who was the teacher of Charles Flahault and therefore, in terms of pedagogical genealogy, a grandfather of Braun-Blanquet.[89]

Nowadays Bonnier is principally remembered for his experimental and morphological work upon topics such as plant respiration and the structure and function of the nectaries. He is often commemorated as a leader of the movement toward an experimental botany. But yet the major part of his work was in floristics and floristic plant geography, as is evidenced by such massive volumes as Flore complète illustrée en Couleurs de France, Suisse, et Belgique (13 volumes in quarto), and Nouvelle Flore du Nord de la France et de la Belgique.[90] He also undertook important studies in Humboldtian plant geography, researching into the action of the environment on vegetation and the distribution of plant associations. For instance, he greatly refined ideas on the parallelisms between latitudinal and altitudinal zonation of vegetation.[91] This had been an important concern of Humboldt himself.

This sort of combination of interests was quite typical of botanists doing Humboldtian plant geography - or ecological plant geography, as it was coming to be known - in the latter decades of the nineteenth century. Ecological plant geography offered botanists the opportunity to ally the old skills of description and classification with the study of process and function. It was, in principle, quantitative. It could be made to involve advanced instrumentation and ways could be devised to study vegetation experimentally - by transplantation techniques, for example, as pioneered by Bonnier.[92] Physiology and morphology, the twin emphases for the New Botany, could both be interpreted ecologically as the responses or adaptations of the plant to the situation in which it grew. Yet ecological plant geography was also an observational science. It also utilised field skills and experience.

Ecologists could thus claim to be fruitfully combining the old and the new forms of botanical expertise:-

> "Thus the ecologist, persuaded of the importance of the various vital problems ... must have a complicated equipment for his varied work; he must be as familiar with the use of the balances, photometric and thermometric instruments, as with the absolute dominion of lifeless nature. In order not to be betrayed into forming hasty conclusions, he must work in the herbarium as a florist, with the microscope as a physiological anatomist ... "[93]

Field-orientated botanists, trained in traditional ways but aware of the decreasing fashionability of traditional botany, found ecological plant geography "a natural outlet for their interests and abilities".[94]

However there were dangers inherent in seeking to lie down with a lion quite as imperialistic as the New Botany. Would its relationship to traditional skills be indeed symbiotic, with the lamb being able to ride, as it were, on the back of the lion toward scientific respectability and status? Or would the lamb find itself assimilated into the body of the beast? Many traditionalists, although interested in modernising field studies, feared that their skills might become entirely subordinate to the new expertise. Oscar Drude, for example, expressed misgivings about the possibility of plant geography being too completely dominated by forms of practice introduced from other sciences:-

> "These [MacMillan's and Warming's] works emphasize the special province of ecology and give preference

> to the methods employed in the organic natural sciences rather than to the methods employed in the geographical. It soon appeared as if the daughter of biogeography would destroy the reputation of her mother and usurp her place, but the opportune appearance of Schimper's work, based upon the same foundation and fulfilling Grisebach's unattainable dream, completely restored the connection between the highly specialized ecological and the broader geographical points of view."[95]

There were important matters at stake here. The imperialism of the New Botany was more than mere rhetoric or the setting out of an intellectual programme. From the eighteen-fifties, the intensely competitive German university system was, as ever, overproducing eager young men, imbued with aggressive professional pride, and possessing doctorates in physiology or some other aspect of the New Botany.[96] The production of New Botanists increased even more in the 1880s.[97] The New Botanists coveted the professional opportunities in general botany. Thus they came directly into competition with recruits more traditionally trained. This was true even in Britain where there were many fewer New Botanists. Joseph Hooker had to advise a friend trained in the 'old school' that he was unlikely to be successful in an application for a chair in botany due to his lack of experience in the new subjects.[98]

It must be remembered that, despite the rise of the New Botany, the training of botanists in more traditional skills did not cease. The teaching of taxonomy did not generally become as moribund as it did in Cambridge under the ageing Babington. The New Botany has received more attention from historians, but Old Botanists, if one may so refer to them, continued to be trained - in some numbers by Engler in Berlin, in lesser numbers in Edinburgh and at various centres in Germany, France and Switzerland.[99] As well as the sheer inertia of a well-established traditional research and pedagogical activity, floristic botany was sustained by its economic importance. The Botanical Gardens and Herbaria of Berlin and London served Imperial interests.[100] Floristic botany was an essential tool in the exploitation of the natural resources of the colonial possessions. The continued existence of taxonomy was assured, therefore, however unfashionable and unglamorous it might seem when compared with the New Botany.

Another problem for the floristic botanists was that, given the intellectual freedom which each professor possessed under the German system, it was possible to establish a reputation in physiology, achieve a permanent position on the strength of it, and then devote one's research efforts to something quite different.[101] One might, if one enjoyed field work and botanical travelling, extend one's physiology into ecology and plant geography, interests which might earlier have been quite secondary. A.F.W. Schimper's career, for example, follows this pattern quite closely. He was, like Bower, a student of Anton De Bary at Strasbourg and of Julius von Sachs at Würzburg. Schimper established his reputation by work on the origin of starch grains and the morphology of epiphytes.[102] But after he gained an extraordinary professorship at the University of Berlin, in 1883 at the age of twenty-seven, he devoted himself more and more to the study of vegetation and plant geography.[103] These studies culminated in the publication of his book Pflanzengeographie auf physiologische Grundlage in 1898.[104] Likewise Haberlandt, who began his research career in physiological anatomy, was able, having achieved a secure position at the University of Graz, to diversify his interests and to begin to investigate the adaptations which tropical environments produced in plant life.[105] The presence of such men within the field of ecology, with their new high-prestige methodology, threatened the respectability of other forms of practice.[106] The old botany, even in its ecological guise, might seem old hat.[107]

Thus ecological plant geography was an area in which the old and the new botany were coming into conflict and competition. As we have seen, representatives of each felt it necessary to defend the relevance and importance of their own forms of expertise. Here it is relevant to note that the students of Schröter and Flahault received, as undergraduates at Zurich or Montpelier, a traditional, taxonomy-based training with comparatively little emphasis on experimentation.[108] Their professors were not famous physiologists or prominent New Botanists. Montpelier, in particular, had an especially strong tradition of floristic research. It had been a centre for taxonomy, in a characteristically French style, continuously since the days of Rondelet. Montpelier was the "ancient capital of

French botany" or as Braun-Blanquet expressed it, "ville classique des botanistes".[109] Braun-Blanquet and his fellow floristic phyto-sociologists were practitioners of a traditionally-orientated botany:-

> "Braun-Blanquet a pu faire son grand travail sur les groupements végétaux parce qu'il était un excellent connoisseur des espèces. Aussi bien sur les haut sommets des Alpes que dans les plaines arides de l'Aragon ou dans les forêts humides de l'Irlande ou du Pays Basque, il se trouvait toujours en terrain connu du point de vue floristique, ce qui lui permettait de travailler sans difficultés."[110]

One of the achievements of the Sigma programme was to carve out a position of central importance for their traditional floristic skills within the framework of twentieth-century vegetation science - thus defusing the threat from the new methodology of the aggressive New Botanists. As we shall see, their rejection of the habitat and physiognomic criteria for determining the association had the effect of a refusal to yield primacy to physiological methods. Their stress on the fundamental importance of floristic methods in ecological investigation was a defence of their own established practice against the claims of a rival professional group.

Polemical statements directed, explicitly or implicitly, against the advocates of a different ecological practice are frequent in the Sigmatist corpus. Such assertions as "Studies of the structure of vegetation without accurate knowledge of the species concerned are scientifically worthless"[111] were not casual or diffuse observations. They were criticisms of the work of other botanists and were responded to as such by the professional rivals of Sigma and Zurich-Montpelier.

Such a response may clearly be seen in an article written in 1910 by the British ecologist, C.E. Moss, who in common with most British ecologists, was unenthusiastic about the central role of an elaborate classificatory procedure in the Zurich-Montpelier method and wished to base vegetation science on the study of environmental factors, either from a physiological or from a geographical point of view.[112] Moss was responding not directly to Braun-Blanquet but to a paper by Gradmann, who had, in 1909, anticipated Braun-Blanquet and outlined a system of vegetational classification based solely on floristic criteria.[113]

Against Gradmann, Moss argued for the importance of the study of the habitat. Moss wrote:-

> "Whilst the goal reached by the two methods - by the floristic method advocated by Gradmann and the habitat method advocated in this paper - must in all cases be the same, the latter method would appear to be more appropriate and indeed more fundamental from the point of view of the study of vegetation as distinct from the study of Flora. The study of vegetation is not a department of taxonomy ... The view advocated by Gradmann should not, in my judgement, supersede the view that the formation must be determined primarily by the investigation of the habitat; but Gradmann's method furnishes an auxiliary and confirmatory test of the formation in all cases of doubtful habitat ... To insist that the floristic composition of the formation is more important than the habitat is to maintain that the effect is more fundamental that the cause."[114]

Habitat factors, being generally quantifiable physical or chemical parameters (altitude, temperature, soil composition and moisture, and so on) were very relevant to the concerns of those who were trying to apply physiology to the field situation. The physical habitat was the field equivalent of the experimental conditions imposed upon the plant in the physiological laboratory. Thus only by the study of the habitat could the results of laboratory experiments be related to plant growth in the wild. To the student of the habitat, every growing plant was an experiment in physiology. The difficulty was discovering what the relevant experimental variables were.

Investigation of the physical habitat had, of course, long been an important concern of Humboldtian plant geography. Moss wished to emphasise the crucial importance of this form of investigation. But Gradmann, Braun-Blanquet and the other new floristic theorists wished to shift the study of habitat factors from pride of place in the study of vegetation.

The phytosociologists did not, however, wish altogether to eliminate the study of the habitat from vegetation science. Such study was to be a sub-branch of phytosociology entitled 'synécologie'.[115] Synecology occupied a good portion of Braun-Blanquet's book Pflanzensoziologie. He did original research in this area.[116] But, if Moss's views on habitat delineation are contrasted with those of Braun-Blanquet, it will be obvious that what each regards as the logical and necessary starting point of vegetation science is directly the opposite of the other's view. To Braun-Blanquet, the plants themselves were the most reliable indication of the physical conditions:-

> "The most recent grouping of plant communities, according to similarity of floristic composition, proceeds from confirmed observation that every species - indeed every race - has a definite greater or lesser indicator value."[117]

Thus, the only reliable way to identify habitats was by the study of the floristic composition of plant communities:-

> "When a plant community, an association or a sub-division of it, is recognised and floristically circumscribed, the investigation of the habitat and habitat factors must be undertaken."[118]

To Moss, the study of floristic distinctiveness allowed the investigator "an auxiliary and confirmatory test" that he was on the right lines in his investigation of habitat. Direct study of the habitat came first.[119]

These differences between Moss and the Sigmatists correlate with the closeness of the relationship between vegetation science and taxonomy, seen as desirable in each case. Moss, as we have seen, wished to distinguish taxonomy from the study of vegetation:-

> " ... it would be better to refer to the minor differences in habitat as well as to the differences in floristic composition in all definitions of the association. By doing so, the main object of the study of vegetation would be emphasized; and a tendency - by no means an imaginary one - to regard plant geography as a branch of floristic botany would be checked."[120]

Clements and the model of physiology

If taxonomy was Braun-Blanquet's model science, F.E. Clements chose quite a different example to follow. Whereas Braun-Blanquet's professor had been a traditionalist floristic botanist, Clements's professor, C.E. Bessey, was in the vanguard of the introduction of the experimental New Botany to America, and did much to promote the new experimental disciplines of plant physiology and pathology, as well as the field discipline of plant ecology, in America. Bessey saw the German New Botany as having the resources to transform the study of botany in America, enhancing its professional status in the scientific community and its practical value to the larger community as a whole.[121] To Bessey's students, in contrast to Schröter's, German plant physiology carried not a threat but a promise. Not surprisingly, Clements chose German models for his ecology.

Firstly, the work of Oscar Drude was used as the basis for Clements's and Pound's The Phytogeography of Nebraska:-

> "It goes without saying that the writings of the German phytogeographers which have appeared in recent years have been a chief source of inspiration. In particular the admirable Pflanzengeographie von Deutschland of Dr. Oscar Drude has made light the darker places in our path by the copious illustrations and comparisons which it furnishes. It will readily be perceived that the writings of Dr. Drude ... have been made use of in the methods employed. We have departed from his methods only with reluctance, and only in cases where the peculiar circumstances of our region appeared to make it imperative."[122]

Drude was not as physiologically-orientated as many other German ecologists. Indeed, as we have seen, Drude had expressed misgivings as to ecology becoming wholly a province of physiology to the complete exclusion of geographical studies. But his Deutschlands Pflanzengeographie was the ideal exemplar for Clements and Pound. Drude's comparatively simple techniques could be duplicated by the poorly-equipped young graduate students of Nebraska, and yet such techniques carried the full prestige of Germanic science.

Secondly, Clements eagerly embraced physiology - the quintessence of the German New Botany - as the appropriate model science for ecology. Indeed he went further:-

> "There can be little question in regard to the essential identity of physiology and ecology. This is evident when it is clearly seen that the present difference between the two fields is superficial. Ecology has been largely the descriptive study of vegetation; physiology has concerned itself with function; but when carefully analyzed both are seen to rest on the same foundation ... The growing recognition of the identity of the two makes it desirable to anticipate their final merging, and to formulate a system that will combine the good in each ... In this

> connection it becomes necessary to point out to ecologist and physiologist alike that, while they have been working within the confines of the same great field, each must familiarize himself with the work of the other ... The ecologist is sadly in need of the more intimate and exact methods of the physiologist; the latter must take his experiments into the field, and must recognize more fully that function is but the middleman between habitat and plant. It seems probable that the final name for the whole field will be physiology ... "[123]

In Clements's field techniques, measurement of the physical parameters of the habitat was of primary importance - for which purpose he often employed automatic recording devices - mimicking the 'exact methods' of the physiologist. He continually stressed the importance of experiment in ecology. Physiology was the study of adaptation, experimentally and quantitatively, in the laboratory. Ecology was to be the study of adaptation, descriptively, experimentally and quantitatively in the field.

As we have seen, formations, in Clements's opinion, occupied a definite habitat and exhibited a uniform physiognomy. Clements argued that this was due to the fact that physiognomic form was a direct expression of physiological adaptation to the physical environment. To Clements, the habitat was the cause and the vegetation the effect, and in describing the relationship between the two he employed the stimulus-response vocabulary of the physiologist:-

> "The amount of response to a stimulus is proportional to the intensity of the factor concerned. This does not mean that the same stimulus produces the same response in two distinct species or necessarily in two plants of the one species. In these cases, the rule holds only when the plants or species are equally plastic. For each individual however this quantitative correspondence of stimulus and response is fundamental. It is uncertain whether an exact or constant ratio can be established between factor and function; the answer to this must await the general use of quantitative methods. There can be no doubt, however, that within certain limits the adjustment is proportional to the amount of stimulus ... "[124]

Despite all his physiological rhetoric and his stress on instrumentation, it must be stressed that Clements routinely undertook very detailed floristic study in the course of his ecological investigations. It might be said that his ecological practice was, in actuality, based on floristic analysis quite as heavily as Braun-Blanquet's was. Clements devised the metre quadrat and the transect technique to facilitate objective and quantitative analysis of the species composition of plant communities. The implications of his programmatic pronouncements were not necessarily borne out by his actual practice. But the point I am seeking to make here is that, in making programmatic pronouncements as to what ecology should be and what its place among the sciences was, Clements was keen to associate ecology with the obviously scientific and prestigious New Botany subject of physiology rather than old-fashioned floristic botany.[125]

Although his everyday research practice was firmly based upon the study of species composition, Clements was scathing as to the deficiencies of a vegetation science structured primarily upon floristics and upon the individual species as an ecological entity:-

> "The earliest and simplest development of the subject was concerned with the distribution of plants. This was at first merely an off-shoot of taxonomy, and, in spite of the work of Humboldt and Schouw, has persisted in much of its primitive form to the present time, where it is represented by innumerable lists and catalogues. Geographical distribution was grounded upon the species, a fact that early caused it to become stereotyped as a statistical study of little value ... The fixed character of the subject is conclusively shown by the fact that it still persists in almost the original form more than a half century after Grisebach pointed out that the formation was the real unit of vegetation and hence of distribution."[126]

Clements's attitude to taxonomy could not be more different from that of Braun-Blanquet, to whom taxonomy was a body of established knowledge on which vegetation science could rely. In Clements's view, ecological research had shown orthodox taxonomy to be to a large extent erroneous and in need of reform.[127] He prescribed the use of experimental methods in species-making, and demanded that taxonomic categories coincide with those which are useful to the ecologist in the field. 'Experiment' was the shibboleth of the New Botany and the key to its claims for an exalted scientific status. Clements was constantly at pains to portray ecology as essentially an experimental subject - in stark contrast to herbarium taxonomy with its 'medieval' methods:-[128]

> "If taxonomy is to be helpful to anyone but taxonomists ... it must recognize the field as the only adequate place for determining new forms, and must commit itself unreservedly to the methods of statistical and experimental study."[129]

In other words, taxonomists must virtually become ecologists.

Thus the dependence relation between vegetation science and taxonomy that we find in Braun-Blanquet is quite reversed. In Clements's scheme of things, ecology took precedence over taxonomy in the validation of knowledge. In effect, ecologists (or taxonomists whose methods were ecological ones) were to do experiments which would decide what were to count as good species, whereas herbarium taxonomists were merely to document the results of these experiments:-

> "For the preservation of the results obtained by the ecologic methods ... an evolution harbarium is proposed. It is felt that the usual taxonomic herbarium will have its usefulness restricted more and more to the preservation of types, and to the purposes of instruction. The evolution herbarium will be the record of field observations and experimental results ... the evolution herbarium is still to be regarded as a record merely. It is not to replace the taxonomic herbarium as a mass of working material to be shuffled about and made into species. It is a repository of species and forms when they have finally been determined by experiment."[130]

One reason why Clements was so anxious to reform taxonomy was his annoyance at the tendency of the taxonomists of his day to employ a narrow species concept, encompassing little morphological variation. Since the demise of Asa Gray, American taxonomy had become notorious for its domination by 'splitters'.[131] The splitting of established taxonomic categories had led to a multiplication of the number of species and genera in the regional Floras. The subtle distinctions between the newly-created taxa frequently required special expertise to discern:-

> "The field worker must deal with units which are recognizable in the field with a fair exercise of patience and keenness. He must carry in mind the names and characteristics of a large number of species, and he can do this only by relating them to each other.

> There is a very definite limit to the average memory, and this limit is greatly overstepped by a system which trebles the total number of species in a region and substitutes for a clearly marked genus like Astragalus 17 genera recognizable with difficulty by the systematist and practically impossible for others."[132]

Clements's dislike of this practice was shared by Bessey and by his fellow ecologist, H.C. Cowles, of the University of Chicago. All three vehemently expressed their disapproval of splitting tendencies in American taxonomy at the Botanical Congress of 1908.[133]

Acceptance of a narrow species concept would necessarily have involved the ecologists in intensive floristic investigations and would have diverted their attention from the study of the physiological and habitat correlates of species and vegetation-types. And most importantly of all, it would render popular communication and practical application of ecological research more difficult:-

> " ... systematic biology [must] aid and not hinder the development of ecology and the closely related practical sciences of agriculture, horticulture, forestry, plant pathology, economic zoology etc. ... It must recognise that a manual which can be used with success only by the systematist fails signally in its purpose and be willing to construct keys and descriptions primarily for foresters, agronomists, grazing ecologists, and others whose knowledge of taxonomy is slight."[134]

The context of science in the Middle West

To understand why communication with the layman, the forester and the agriculturalist was important to Clements, one must know something of the context of academic science in the Middle West.

The University of Nebraska was a Land-Grant college. The character of the science done in the Land-Grant colleges was very closely defined by its social context.[135] In particular, the colleges were dependent for support upon a lay constituency. To finance their research and keep their jobs, the faculty members had to justify their expenditure of public money in cost-effective terms. The botanists and ecologists had to represent themselves as doing work which would have direct application to agriculture and land management. Bessey, for example, was very active and influential in redirecting American botanical research so that academic botanists began to take seriously the study of the cultivated varieties of plants, of plant pathology and other similarly useful topics.[136] He was also much interested in the study of the vegetation of Nebraska and in the application of vegetational knowledge to practical problems.[137] He investigated, for example, the migration of introduced weed species such as the Russian thistle within the state, and the problem of utilising the prairie grasses for forage. Furthermore, Bessey maintained that finding out how the prairie 'worked' in terms of the composition and dynamics of the plant communities would lead to more reliable guide-lines as to appropriate land use and management.[138]

Clements was likewise throughout his entire career concerned to present his work as applicable and orientated toward the problems of farmers, foresters, and grazers. In sharp contrast to Braun-Blanquet, Clements had direct professional involvements in applied botany. Between 1893 and 1896, he worked part-time for the U.S. Department of Agriculture, while still a student or an assistant professor.[139] A series of other such appointments occupied him throughout his life. In Research Methods in Ecology, published in 1905, Clements made explicit the intimate connection he saw between ecological research and practical concerns:-

> "Forestry ... is the ecology of a particular kind of vegetation, the forest.... whatever contributes to the ecology of the forest is a contribution to forestry ... A full knowledge of the character and laws of succession will prove of the greatest value to the forester in all studies of forestation and reforestation. Forests which now seem entirely unrelated will be seen to possess the most intimate developmental connections, and the fuller insight into the life-history gained in this way will have a direct bearing upon methods of conservation, etc."[140]

Clements continued to combine interests in pure and applied research after he went to Minnesota. The University of Minnesota was also a Land-Grant college and the same social pressures shaped the activities of faculty members as at Nebraska.[141] Clements was from 1907 to 1910 an adviser with the U.S. Forestry Service.[142] And, as Minnesota State Botanist, he organized the Botanical Survey of Minnesota on an ecological and practical basis:-

> " ... a knowledge of soil and climate and of the plant's relation to them is necessary to determine what primary crop, grain, forage or forest is best. For the farms of the State, the best use is a matter of knowing the soil and climate differences of regions and fields, and taking advantage of these in crop production. For the unoccupied lands of Minnesota, we need a classification survey to determine the best use of the different areas, to prevent the waste of human effort and happiness involved in trying to secure from the land what it cannot give, and yet to insure that the land will reach as quickly as possible its maximum permanent return. For occupied lands, the study and mapping of soil and climatic conditions would constitute a use survey of the greatest value in adjusting plant production to the conditions which control it ... Such a division would be determined primarily by studies of soil and climate, necessarily supplemented by the evidence of native vegetation itself ... "[143]

During his period with the Carnegie Institution, Clements's concern with presenting ecology as an applicable form of pure research was, if anything, stronger. Unlike some other Land-Grant college or agricultural experiment station personnel (such as Wisconsin's E.V. McCollum or Raymond Pearl, also a student of Bessey's), Clements did not relinquish all interest in his lay constituency upon leaving the Land-Grant colleges and entering an independent institution.[144] Ecology, more than genetics (Pearl's specialty) or physiological chemistry (McCollum's), had within it an important role for the popular technocrat which Clements did not renounce. Plant Indicators, which Clements produced in 1920, was entirely devoted to the theory and practice of using vegetation as a guide to agricultural practice and land management.[145] In it he gave his opinion on matters such as the value of coyote-proof fences for lambing-grounds and the relative advantages of various methods of sheep herding.[146] Most significantly of all, he set out what he regarded as the case for an official use classification of the lands of the West.[147] He recommended the essentials of a grazing policy - going to the extent of quoting, in full, the grazing bill which William Kent, Congressman for California, presented unsuccessfully to the House of Representatives in 1913.[148]

The immense agricultural and social problems of the Great Drought in the Plains States made Clements even more prominent in an applied capacity. In 1933, Clements was requested by the Director of the Carnegie Institution to place himself at the service of the Government agencies dealing with erosion problems on the plains, and he served as a consultant to the Soil Erosion (later the Soil Conservation) Service, until his death.[149] He also advised the Great Plains Drouth Committee as to, as his wife put it, "whether the farmers of the Dust Bowl should be unsettled, resettled, subsidized, taught how to farm, or be painlessly chloroformed".[150] Clements made detailed recommendations as to how the Plains should be used:- the Southwest and Great Basin set aside entirely as wilderness, the Western Ranges to be non-arable, ranching country and only the more humid east to be farmed. The Great Plains Committee reported to President Roosevelt in 1936.

In the era of the Dust Bowl and the New Deal, Clements was keen to make evident the practical utility of his work. This is obvious from an article he wrote in 1936 entitled "Experimental Ecology in the Public Service".[151] His belief in the applicability of technical ecology to mundane practical matters is well illustrated by the following quotation:-

> "In the three great aspects of the shelter-belt project, ecological considerations necessarily reign supreme. The method of indicator communities is indispensable to the selection of site and species, and it may be epitomized in the statement that climax areas are the most difficult of conversion and control, while seral, subclimax and postclimax sites hold out the greatest promise. The preparation, development and maintenance of the wind-break communities are almost wholly dependent upon the understanding and control of such processes as reaction and coaction, in which man may easily become the adverse element through omission or commission."[152]

There can be no doubt that the applied orientation of the Land-Grant faculties 'pre-adapted' Clements and his ecology to play an important role in the national re-orientation of attitudes towards land use and land management which was occasioned by the Great Drought and the Dust Bowl.[153] The era of the New Deal was the zenith of ecology's involvement 'in the public service', but the giving of advice to farmers, grazers and management agencies had been a major concern of Clements throughout his working life.

Such interests were not idiosyncratic to Clements but were required of any scientist in his institutional position - whether at Nebraska or Minnesota or indeed, latterly, at the Carnegie's Western laboratories. Such was the importance of the lay audience upon the Land-Grant colleges, and indeed upon American science generally.[154] Also it might be said that Clements inherited such interests from Bessey and shared them with other students of Bessey such as H.C. Shantz, N.E. Hansen and J.E. Weaver.[155] All these men were subject to the same contextual pressures and their activities and professional legitimations were moulded in similar ways.

There was, however, a difficult balance to be found here because it was also incumbent upon the ecologists of the Mid-West that they were not seen to be devoting themselves entirely to application and such matters as keeping the coyotes from the lambing ewes. Otherwise their status as scientists within the discipline of botany would suffer.[156] Clements may be said to look always in two directions; one was toward the lay constituency in which he sought the status of a respected technical adviser, and the other was toward the ideal of disinterested science in the European mode - an ideal sustained in American plant science by the universities and museums of the East and sustained for Clements by his professional attachment to the discipline of botany. Equally as hard as he sought to convince his lay constituency of the value of ecology in practical application, Clements sought to establish ecology as an important and respected branch of botanical science. He wrote to Tansley shortly after the publication of Research Methods:-

> "You will have gathered from the text how deep my desire is to see ecology fashioned into a real science ... Most of my American colleagues are still very much at the "descriptive ecology" stage."[157]

Accordingly, Clements argued that ecology must become rigorously experimental and (in the light of Clements's concept of the scientific) well-codified and deductive.[158] Hence his concern for strongly deductive laws of vegetation. Hence the rhetorical importance of his modelling of ecology upon the indubitably scientific subject of physiology. Hence the concern for a standardised terminology for vegetation, strictly and ostentatiously derived from the classical languages.[159]

Furthermore, ecologists must reflect upon their methodology:-

> "There is no other department of botany in which the superficial study of more than half a century ago still prevails to the exclusion of better methods, many of which have been known for a decade or more."[160]

and gain the objectivity associated with the use of instruments:-

> " ... it becomes necessary to appeal to instruments, in order to determine the exact amount of each factor that is present in a particular habitat ... The employment of instruments is clearly indispensable for the task which we have set for ecology, and every student that intends to strike at the root of the subject, and to make lasting contributions to it, must familiarize himself with instrumental methods. One great benefit will accrue to ecology as soon as this fact is generally recognised. The use of instruments and the application of results from them demand much patience and seriousness of purpose upon the part of the student. As a consequence there will be a general exodus from ecology of those that have been attracted to it as the latest botanical fad, and have done so much to bring it into disrepute."[161]

Ecology must be made scientifically respectable.

But, given the necessary context of research in the Land-Grant colleges, ready communication between scientist and layman, and an obvious concern with the layman's problems were also demanded. The difficulties of this balancing act are well illustrated by the plight of Conway McMillan, Clements's predecessor at Minnesota. McMillan had been forced by the local reception of his first book _The Metaspermae of the Minnesota Valley_,[162] to modify the style and content of his writing. He next produced the much more readily accessible _Minnesota Plant Life_, which was an applied text in the sense that it could be used in the high school classroom.[165] McMillan confided in Clements that he made this shift because the administrators at the University of Minnesota were not "terribly fond of erudition".[164]

McMillan's study of the shoreline vegetation of Lake of the Woods was a major piece of ecological research.[165] It was the first American ecological work to receive wide acclaim. Oscar Drude ranked it on a par with Warming's great book _Lehrbuch der Ökologischen_

Pflanzengeographie.[166] But such work gained him little honour in his own country, and eventually McMillan, frustrated with his conditions of work at Minnesota, abandoned botany altogether.[167]

It is evident that it was unwise in the context of the Land-Grant colleges to indulge oneself in unduly esoteric research. Significantly, the German model of scientific activity was explicitly rejected by certain figures influential in the direction of science in the West. E.W. Hilgard, Director of the California Agricultural Experimental Station, wrote:-

> "I do not believe that a station so situated ought to make it their business to pursue recondite studies in vegetable physiology or animal chemistry, unless they have first satisfied this legitimate demand [applicability]."[168]

Ready communication with the lay constituency was vitally important.[169] As we have seen, such a requirement was partly the cause of Clements's quarrel with the splitting taxonomists. As well as complicating ecological field research, a narrow species concept would, if generally adopted, make communication between scientist and lay land-users more difficult. However the broader Grayian species-concept involved the recognition as species (or at least as genera) of many of the floristic categories of colloquial speech, such as the flowers and shrubs recognised by farmers and forestry workers.[170] It is understandable that it was with this sort of species-concept that Clements, Bessey and Cowles wished to work.[171]

It is readily understandable, also, that the Clementsian units of vegetation were virtually the same in terms of extent and important identifying characteristics as those of the farmer, the grazer, and the range manager. Tall-grass prairie, short-grass prairie, true prairie were categories of prairie easily recognisable by laymen being, in fact, quite similar to the layman's own classification.[172] There must have been little incentive for Clements to adopt a more esoteric unit of vegetation.

The terminology which Clements employed, and in many cases invented, to describe these units of vegetation and the relations between them, was dense with neologisms and complex to the point of obscurity.[173] But the expert must be careful not to speak exactly the same language as his client; otherwise the client may doubt the need for the expert. The important point to note here is that Clements's classification was readily translatable into lay terms and thus readily communicable to non-experts. Foresters, for example, continued to speak to their clients in Clementsian terms, if not quite full Clementsian terminology, for many years. For instance, in 1948 E.I. Roe, silviculturist at the Kawashiwi Experimental Forest described the natural forest vegetation of the Great Lakes in the following manner:-

> "These types consisted ... of the two climatic climax associations - the deciduous or maple-bass wood, and the coniferous or spruce-fir and the various edaphic climax associations such as elm-ash-soft maple, pine, oak-hickory, etc. As you know, the latter type of climax eventually will be succeeded by the climatic climax types. However this succession requires so long a period without disturbance that to foresters the edaphic types are fully as important as the climatic ones."[174]

Inherent in these statements was much Clementsian theory such as the assumption of a climatic monoclimax, long successional processes displacing edaphic associations and the uniform physiognomy of the climax - all expressed by the reference to groupings of tree species, easy for the layman to identify and comprehend.

In contrast, the Sigmatist classification of vegetation diverged markedly from lay practice. For instance, M. Guinochet's classificatory map of the vegetation of Pontardies has a large expanse of Fagetum without a beech tree to be found on the ground, but dominated by spruce and with beech-association character-species in the under-storey.[175] His classification is quite misleading to the uninitiated, whereas Clements's units are quite plain.

As well as being more esoteric, the European units of vegetation were much smaller in size that those employed in America. But in Europe investigation on a small scale was feasible. The Flora was well worked out; the distances to cover were comparatively short; the available man-power, in terms of trained botanists, comparatively large. It was possible for ecologists to sustain intensive research on small area units - which, of course, the vegetation was generally broken up into by topography or human activity. Indeed one might say that, for ecological inquiry in Europe, especially for inquiry based on floristics, a small unit was not only possible, it was professionally convenient. If Europe were to be considered to contain only, say, twenty or thirty associations, how could the relatively large number of newly-trained phytosociologists continue the floristic research programme of their teachers? A small floristic unit which allowed the younger generation to identify and characterise new associations obviously had its advantages.

Pure French science

There was much less pressure from a lay constituency on Braun-Blanquet or on any of the Sigmatists. In Montpelier, they were freer to present themselves as doing pure science for they worked within an institutional and cultural ethos which encouraged such a presentation. H.W. Paul has described how the French, eager to restore the reputation of French science after its mid-nineteenth century comparative decline, developed an ideology of pure, disinterested research in the early years of the twentieth century.[176] This ideology was produced in the context of a national competition with the Germans to be the creative geniuses and scientific pedagogues of Europe. Whereas Germany's scientific output had been in the banausic fields of applied research, France, so the argument went, should cultivate pure research to display French superiority of culture and intellectuality. In 1918, the President of the Académie des Sciences, Paul Painlevé, spoke of the pursuit of science for purposes of immediate utilisation or pecuniary gain as degrading the soul and ending in cultural barbarism:-

> "La science n'est moralisatrice qu'à condition de garder aux yeux de l'élite qui la cultive son caractère essentiel qui est la recherce désintéressée de la verité ... de l'autre côté du Rhin, la Science, c'était une gigantesque enterprise où tout un peuple, avec une patiente servilité, s'achamait à fabriquer la plus formidable machine à tuer qui ai jamais existé."[177]

Painlevé's remarks were directed specifically against the German industrialisation of laboratory science, but were also of general import for French science as a whole. Painlevé's expression may be regarded as rhetorical and hyperbolic but the encouragement of pure research, to be presented as purer research, was real enough. The French ideology of pure science meant that the provincial faculties of science, of which Montpelier was one, were actively discouraged from increasing the practical orientation of many of their courses.[178] Paul also points out how these influences extended into Switzerland where the French were very sensitive of the need to maintain their position and to prevent the complete absorption of the Swiss universities into the German educational system.[179]

However, in the early decades of the twentieth century the French provincial faculties of science had developed strong links with local industry and other commercial enterprises.[180] In Nancy, for example, there were technical schools in chemistry, electrochemistry, agriculture and brewing - all training personnel for local industry.[181] In Toulouse, courses in agricultural and industrial chemistry were inaugurated in 1886 and 1889.[182] A special part of the curriculum at Lille was devoted to the study of the chief industries of Northern France.[183] Similar links between faculty and commerce developed at Montpelier.[184] Often the financial well-being of the provincial institution was dependent upon these links.[185]

Whatever the official ideology of research might be, the provincial faculties were not in a position to abandon applied research altogether. Ideologies of pure and applied research had to be accommodated together. The result in Montpelier was that priority was given to pure research with application being stressed as important but as necessarily consequent upon disinterested research. Thus the Sigmatists did not neglect the practical applications of phytosociology, but they regarded application as secondary to the pure study of vegetation for its own sake.[186] Foresters did come to study at Montpelier and a certain amount of applied research was undertaken under the auspices of Sigma.[187] But generally, students were to come to Montpelier to learn vegetation science which they were to go away somewhere else to apply. In 1932, a second station was set up in Germany under Reinhold Tüxen. Tüxen had a special interest in applied phytosociology. Much of the teaching on applied matters was done under his auspices.[188]

Braun-Blanquet, in marked contrast to Clements, was able to present himself as a scientist doing pure research first and foremost. The firm distinction made at Sigma between pure and applied research and the priority given to pure research may be seen in Braun-Blanquet's text-book:-

> "The analysis of plant communities may follow the purely practical lines of forestry and agriculture or the more theoretical lines of plant sociology. For the phytosociologist, the first task is to carve out and delimit the association, in order to lay the most indispensable foundation for synecological, synchronological and syngenetical investigations ... Problems of the structure of communities, as presented by agriculture and forestry, form in themselves a very comprehensive complex. These can be considered here only in so far as they are related to the structural studies of general plant sociology."[189]

This is virtually the only mention of applied work in the entire text. Such a firm division of pure from applied research is not present in the Clementsian corpus - indeed is virtually unthinkable in the context of Clementsian ecology. Braun-Blanquet did not give his attention to problems of soil erosion, grazing legislation, sheep pens or any of the other applied matters which occupied Clements's attention. Indeed he left Zurich partly because he found the lack of good facilities for pure research at the Ecole Polytechnique to be uncongenial.[190]

Braun-Blanquet did occasionally make programmatic statements as to the relevance of phytosociology "dans la domaine des applications pratiques" - the sort of pronouncements that can be found being made by virtually every scientist who ever tried to attract research funding or ever stood on a public platform.[191] His ideas of practical application for phytosociology include its usefulness not only to commercial activities directly, but to 'pure' subjects like taxonomy, geology and pedology.[192] He was personally involved in few practical projects. He advised on forestry land-use in the Languedoc and, in 1939, he directed the camouflaging with plants of Swiss gun emplacements.[193] When he returned to

France in 1940, he placed himself at the disposal of the Académie des Sciences and the Centre de Recherches Appliquées. He was given the somewhat donnish task of taking pharmacy students on botanical excursions.[194]

Braun-Blanquet was, thus, not involved in practical advisory work to anything like the extent Clements was. His career was not structured around service in forestry and soil erosion service agencies as Clements's was. Nor were the French phytosociologists as a whole as active on the public stage as their American counterparts. There was no French Great Plains Drouth Committee, no Tennessee Valley Authority, no Conservation Corps. The French phytosociologists were not routinely at the beck and call of a lay constituency. The provincial faculties of science had strong links with local commerce but they were not Land-Grant colleges. Despite their dependence on direct contributions from local industry, the French provincial faculties were autonomous to an extent impossible in America. The Land-Grant colleges were State-funded institutions and it was a tenet of American democracy that recipients of public funds were accountable directly to the citizenry from which the funds were drawn.[195] No such principle applied in France. Given Braun-Blanquet's institutional and disciplinary context, there was clearly no pressing need for him or his colleagues and students to speak the language of the farmer and the forester. Hence the feasibility of ecological study based upon a small, esoteric and intuitively unobvious unit of vegetation.

The organismic analogy

We have not yet looked at one important aspect of Clements's conceptualisation of vegetation and that is his persistent analogy between the formation and the individual organism:-

> "The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism, the formation arises, grows, matures, and dies. Its response to the habitat is shown in processes or functions and in structures which are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development."[196]

It was by employing this organismic conceptualisation of the plant community, that Clements was able to argue, in contrast to the Sigmatists, that the formation was a concrete rather than an abstract or ideal entity. All the vegetation in any given area was developmentally related to the climax vegetation type. Therefore it was best considered as part of the same organic entity:-

> "All the stages which precede the climax are stages of growth. They have the same essential relation to the final stable structure of the organism that seedling and growing plants have to the adult individual. Moreover, just as the adult plant repeats its development, i.e. reproduces itself whenever conditions permit, so also does the climax formation. The parallel may be extended much further ... In short, the process of organic development is essentially alike for the individual and the community."[197]

In his earlier work, Clements defined formations purely in terms of vegetation but after 1918 or so, he included the associated animal populations. The principal unit of his ecological system became the 'biotic formation' which "was regarded as an organic unit comprising all the species of plants and animals at home in a particular habitat".[198] However he continued to write about the plant formation as an organism. I will generally confine myself to discussing his plant work. The community organism was sometimes distinguished from individual organisms by being referred to as the 'complex' or 'super-' organism.[199]

There were many holistic schools of thought active in America in the early decades of the twentieth century. Thus by adopting this holistic organismic approach Clements was able to present his views as being in harmony with much of the science and philosophy of his time. He was, for instance, able to claim that his conception of the organismic character of the natural community derived support from the philosophy of Herbert Spencer - which had a huge vogue in America at the turn of the century.[200]

We know from the reminiscences of Roscoe Pound that Clements was reading Spencer with enthusiasm in the 1890s:-

> "I remember how he [Clements] and I used to discuss ... Spencer's "Principles of Biology" of which we had expected great things in the days when Comtian Spencerian positivism was almost a religion to scientists."[201]

In later years Clements was to refer to Spencer's work frequently and with approval - as embodying an organismic conception of social order similar to his own:-

> "Spencer has discussed the concept of the social organism with signal clarity and the student of community development can still turn with great profit to his treatment of this theme."[202]

Another important reference to Spencer is to be found in Clements's essay on the "Social origins and processes among plants" published in 1935 in the Handbook of Social Psychology:-

> "The view that the plant community constitutes an organism of a new order was first advanced in 1901. With the full recognition of the social bond between plants and animals the concept was broadened to apply to the entire biotic grouping which was regarded as including man, under natural conditions at least ... It was later recognised that this view had been foreshadowed in part by Comte (1830), by J.S. Mill (1843), and more particularly by Spencer (1858, 1864), who emphasized certain striking similarities between simple organisms and societies."[203]

Clements also supported his organismic views with reference to more contemporary holistic philosophers such as Whitehead and Smuts.[204] Smuts was himself interested in ecology and, like Clements, in Neo-Lamarckianism, so here the reinforcement was mutual. Smuts wrote:-

> "The new Science of Ecology is simply a recognition of the fact that all organisms feel the force and moulding effect of their environment as a whole. There is much more in Ecology than merely the striking down of the unfit by way of Natural Selection. There is a much more subtle and far-reaching influence within the special or local "fields" of Nature than is commonly recognised or suspected."[205]

Clements also claimed affinity with other holist theorists in the biological and social sciences:-

> "The most recent, and in some ways the most significant, contribution to the concept has been that of emergent evolution, as embodied in the views of Henderson, Spaulding, Sellers, Broad, Morgan, Jennings, Summer and Keller, and Wheeler. While this development has taken place more or less independently of ecology, it is in practically complete accord with the earlier concepts of the complex organism."[206]

Clements was thus able to give his organismic viewpoint most impressively respectable intellectual credentials. The common denominator which Clements pointed to in all these holistic thinkers was their postulation that highly organised entities were more than the sum of their constituent parts. He quoted with approbation the following passage from Summer and Keller's The Science of Society:-

> "Human society then, by the diversity of its parts, their specialisation, the distribution of functions, the mutual service and support of the parts and their solidarity, is a true system or oganization. It has a life different from that of the individual. The quality of a combination is not the sum of the qualities of its components. There is a body to study as well as a cell, a society as well as an individual; and the body and the society are things with lives and laws of their own. Hence forces arise in the societal organisation which are characteristically societal forces."[207]

Thus the plant community might be conceived of as possessing, like Wheeler's insect societies, 'emergent' properties in this sense. One might say that it was greater than the sum of its constituent plants:-

> "One of the first consequences of regarding succession as the key to vegetation was the realisation that the community ... is more than the sum of its individual parts, it is indeed an organism of a new order."[208]

One reason for the organismic analogy being convenient for Clements to employ was that, as in the above quotation, it enabled him to speak of 'development' in a sense which mimicked the discourse of the more prestigious branches of biology. Studies of the development of the individual organism had lately proved very fruitful for students of morphology and phylogeny:-

> "I hope you will ... feel that my proposals in regard to the formation offer the opportunity of putting us on a real and permanent scientific basis, such as development had made possible or is making possible in [word indecipherable] other botanical fields."[209]

Furthermore, it strengthened the comparison Clements sought to make between ecology and physiology. Ecology could be represented as studying the structures and functions of the complex organisms in an analogous manner, and with equally exact methods, to the way physiology studied the structures and functions of the individual organism.

Organicism and ideology

But to understand fully the useful work that this conceptualisation of the plant community did for Clements, one must understand something of the social and political background of agriculture and land-use on the Great Plains, and how Clements sought a particular role for himself and his science within that context.

The Great Plains, treeless, dry and bare compared to the Eastern and Western seaboards, and initially unattractive to the homesteader, were first utilised by the white man as ranching country.[210] From the eighteen-forties onwards, the vast area of what is now Western Texas, Oklahoma, Kansas, Nebraska, North and South Dakota, Montana, Wyoming, and much else besides, virtually all the semi-arid grassland, was exploited as grazing for cattle. The cattle were allowed to range over huge acreages which were not fenced. The men who owned the cattle often had no property rights over the land the cattle grazed. Almost all of it was Public Domain - part of the vast tract of land held purely passively by the Federal Government. Anyone who could gain access to sufficient water to supply a herd could set up as a rancher. Inevitably this system led eventually to overstocking and, frequently, to lawless rivalry between jostling cattle barons. Overgrazing became endemic since if any part of the range was not obviously fully utilised, someone else would put down his own cows there. The consequent shortage of grass seemed to be serious enough to place in doubt the continued viability of beef production.[211]

In 1862, the Federal Homestead Act was passed. This allowed small farmers to gain possession of land on the Public Domain simply by the acts of settling on it and cultivating it. The Act was passed during the Civil War to strengthen the ranks of the yeoman farmer, a class of citizen invested with special ideological significance by many American politicians, especially Yankee ones, as the essential bulwark of American individualism and republican democracy.[212]

By the eighteen-eighties, just as the overgrazing on the ranges was becoming acute, the homesteaders were beginning to encroach upon the Great Plains.[213] They were brought there by the ever-increasing population pressure within the United States, the exhaustion of homesteading opportunities in timbered provinces and the invention of cheap methods of fencing. Quite large areas of the grassland, the river-valley bottoms and the tall-grass prairie, could be homesteaded successfully, but ever-increasing pressure of numbers forced settlers to occupy land on which arable farming, as then practised, was problematic due to lack of precipitation, or underlying light or sandy soils, or both. In these areas the small farmers failed as often as, indeed more often than, they succeeded. The homesteading frontier swayed backwards and forwards as a few dry seasons followed a few wet ones or vice-versa.

Aridity was not, however, the only problem faced by small farmers in the eighteen-eighties and -nineties. Structural changes in the American economy were shifting the locus of national economic power.[214] Agriculture was no longer as predominant as it had been. The economic importance of the industrial cities was rapidly increasing. Even relatively successful farmers no longer wielded purchasing power on a par with their urban equivalents. Agricultural discontent came to a head with the collapse of farm prices during the depression of 1896.[215]

The numbers of impoverished, displaced, or merely discontented homesteaders created real political and social problems. They demanded help from State and Federal government - help which the governments were often reluctant or unable to give.[216] The very strength of the farmers was held to be their rugged independence and self-sufficiency. Nothing, it was said, must be done to weaken these virtues. Also there were, at the time, formidable constitutional obstacles in the way of spending public funds to aid or support any particular group. American government was minimalist and entrenched in laissez-faire. And the farmers' lobbies, although they demanded intervention when times were poor, opposed it equally vehemently when it threatened to circumscribe their right to settle where they liked and farm how they liked, or when it seemed to imply a weakening faith in the homesteading ideal.

There were other problems peculiar to the arid lands. Most pressing of all was the legal one of water rights.[217] Under the law which pertained in the East, water belonged to whoever owned the land upon which the water happened to be. But in a dry country this principle gave farmers and ranchers the right to fence off water holes and dam streams, ensuring water for their own crops or herds but condemning their neighbours to failure. Cattle men fought (often literally) with farmers as well as each other over access to water, to droving trails, to feeding areas on the trail and simply for space on the range. The individualistic location of water and other land rights meant that the setting-up of collective or public irrigation schemes, essential if the arid lands were to be developed to their full arable potential, was greatly hindered.

All this was aggravated by the general lack of legal or political recognition of the rights and needs of the cattlemen. The Homesteading Act envisaged small farms of a few hundred acres; the cattlemen required units of thousands of acres. The cattlemen did not have a place of honour in the political consciousness of the nation like that accorded to the yeoman farmer. The large-scale ranchers were regarded by many merely as obstacles to the establishment of prosperous farming communities. The ranchers claimed that they were misunderstood by the Eastern legislators.[218]

By 1902, with the passing of the Newlands Act, the situation over water and irrigation was improved with a new legal principle of collective right to water being established for the Western States. The range and wire-cutting wars were over. But the problem of establishing a stable pattern of utilisation for the plains was not yet solved. The failure rate among the homesteaders on the dry lands was very high. Between 1890 and 1910, at least one out of every two new homesteads reverted to the public authorities within five years.[219] In Nebraska, the proportion failing was even higher. The grazing pressure upon the land not yet ploughed was becoming more intense. These problems were to grumble away until the new legislative attitude of the New Deal.[220]

This was the situation within which Land-Grant ecology emerged in the 1890s and 1900s and within which Clements and Bessey's other students were called upon to help the individual farmer and cattle-rancher to maximise their returns. But such a context of problem and conflict conjured for the ecologists the alluring image of a grander field of exercise for their skills - the scientific management of the plains grassland as a whole. Objective expertise could sit above factional interests and promote scientific efficiency where previously there had been disorder, strife and wastefulness.

Such a prospect was particularly alluring because the scope of ecology was thereby enormously widened and the power of its practitioners correspondingly increased. To achieve the optimal exploitation of the plains would clearly involve the direction of human as well as natural resources. The ecologists would be called upon to advise not just upon the digging of draining ditches and the uprooting of Russian thistles, but on the very structure of the agricultural society itself. Clements expressed the ecologist's new vision of the scope of his subject:-

> "Because of the synthesis inherent in it, ecology is also to be regarded as a point of view and a method of attack for various great biological problems. Not only does it concern itself more or less with the whole of biology, but it also must ... make basic contributions to the practical sciences of agronomy, horticulture, forestry, grazing, entomology conservation, etc., to say nothing of education, economics, sociology, and politics."[221]

Ecology was thus presented as a powerful synthetic science, able to guide all aspects of man's interaction with his natural environment.[222]

In many ways the doctrine of the ecologist as expounded by Clements was no different from that articulated by the advocates of State forestry, mineral leasing legislation, anti-trust laws, or any of the other touch-stones of Progressivism. In all these areas, the problems were seen as the consequence of individualistic and unrestrained economic behaviour. Collective action guided by scientific expertise was the answer.[223]

The imposition of centralised technical planning and direction when previously the individual or the corporation had cared only for itself was the common rhetorical demand of reformers in the generation which sought to heal the social wounds of laissez-faire. The appeal was routinely made that the larger welfare of society as a whole should take precedence over that of the individual, and that individual activity should be so directed that it would serve rather than harm the common good. The way to maximise social harmony and economic success was to take the broader view. Hence the need for a synthetic and socially-aware perspective in the management of natural resources.

As William Akin has pointed out, within the general context of Progressivism, this holistic, scientistic and centralising credo was first and foremost the ideology of the planner and technocrat.[224] Scientific expertise, it was claimed, was not tainted by interests and thus scientists could best perceive where the fairest course lay. Furthermore, scientists had privileged knowledge of nature and could thus, as Frederick Winslow Taylor put it, "bring about the realisation of social harmony through ... the organisation of human affairs in harmony with natural law".[225]

Technocracy has been characterised as an ideology of engineers - for whom it provided the promise of enhanced status and influence.[226] I would argue that ecologists should also be regarded as aspiring technocrats in their own field. The Ecological Society of America captured the spirit of technocratic rhetoric well when it resolved that college courses in ecology should seek to:-

> " ... inculcate and inspire a broad and synthetic point of view that will enable students to see the problems of natural resources, not as separate and discrete, but as parts of a single master problem of how best to administer nature as a whole."[227]

Similar sentiments were expressed by the members of the animal ecology group, which in the 1930s and -40s gathered around W.C. Allee at the University of Chicago. These men shared Clements's belief in the importance of regarding the biotic community as an organismic whole.[228] Clements had links with the Chicago group in that he wrote a textbook jointly with Victor Shelford, Professor of Zoology at the University of Illinois.[229] Shelford had been a student of Cowles at Chicago and had combined the plant ecology of Cowles with the behavioural studies of C.O. Whitman to produce some of the earliest animal ecology done in America.[230] Before moving to Illinois, Shelford had been on the faculty at Chicago where W.C. Allee had been his first graduate student. He was pleased to refer to the "slow but gradual recognition of the importance of the concept [the community as a unit]" as partly being due, as far as the animal side of ecology was concerned, to the activities of his students.[231] We may assume that the views of Clements, Shelford and Allee on the biotic community were broadly similar.[232]

Donald Worster has recently made the following suggestive remarks on the subject of the Chicago animal ecology group:-

> "'The organismic-community concept of modern ecology', the group suggested at one point ... 'is one of the fruitful ideas contributed by biological science to modern civilization' and certainly it was a chief inspiration in their search for what Emerson [Alfred E. Emerson, a prominent member of the Chicago group] called a 'scientific basis for ethics'. Their earlier, less-known writings stressed this quest even more strongly. There, they openly, sometimes dogmatically, strove to extract from nature a set of holistic values to apply to mankind."[233]

As Cynthia Russett has pointed out, Alfred Emerson's was a "striking ... example of deliberately normative equilibrium theory".[234] The Chicago group regularly argued from what nature was to what human society ought to be. They stressed the great reward that would accrue from harmony with nature. Emerson's favourite slogan was 'dynamic homeostatis' - a characteristic to be found only in highly integrated systems, 'organisms' in his terminology:-

> "Many terms and phrases carry implications of homeostatis and indicate that the concept is old. These include such words and phrases as beneficial, well-being, adaptation, adjustment, welfare, security, harmony, equilibrium, balance, the good life, satisfaction, prosperity, enrichment, self-fulfillment, the full life, self-sufficiency, progress ... contentment and happiness."[235]

Ecologists thus presented themselves as the experts who could manage nature along nature's own guidelines and thus make Man's dealings with nature as harmonious as the image of nature which their rhetoric conjured. A holistic rhetoric based on the harmonious qualities of nature served to legitimate the experts' challenge to the private and sectional expediencies which had led to so much social disruption.[236]

Here it might be objected that the social metaphor used by, for example, the engineers within the technocratic movement was not that of the organism but that of the smoothly running intricate machine. But, despite the endemic disputations in the general history of biology between organismic and mechanical conceptions, too much should not be made of this distinction in the present context.[237] The important point is that both images were holistic ones, invoking a harmonious arrangement of human affairs in accordance with natural laws. An organism, like a machine, could be described as "a system of interlocking ... processes, interdependent and delicately balanced, in such a way that the due working of any part of it is conditional on the due working of all the rest".[238] Both models legitimated the role of the expert in charge since he alone understood the natural laws which governed the functioning of the complex holistic structure. It was natural, one might say, for an engineer to pick a mechanical metaphor, and for a biologist to pick an organismic one, but the rhetorical function of the two conceptions was identical. And indeed the two models had common elements. Clements, for example, spoke about vegetational "dynamic equilibrium" in quite a mechanical sense.[239]

This lack of fundamental difference between Clements's organismic model and a mechanistic one leads us to an important insight into the nature of Clements's conceptualisation of vegetation. Clements was at some pains to point out that there was nothing mysterious, mystical or vitalistic about the properties of the vegetational superorganism. It was a concrete entity. It obeyed the laws of physics and chemistry as well as the natural laws of vegetational development. It had a cause-and-effect relationship with the physical environment. It was a very mechanistic, natural-law sort of emergent holistic organism. The social integration between the plants was not the product of psychic sympathies or underlying teleological principles, but, as in Spencer's theory of the social organism, was the product of the intense competition between individuals.[240] Mutualism arose as a result of competition. Clements's formational organism was very far from the vitalistic, inherently and all-encompassingly mutualistic conceptualisation which certain authors have detected in other ecologists such as Robert Smith, a British botanist roughly contemporaneous with Clements.[241] Clements identified and opposed such opinions in certain of his American contemporaries:-

> " ... several American botanists ... without a shred of proof hold firmly the view that there is an "undiscovered vitalistic something" in competition."[242]

It ought also to be noted that although Clements supported the conception of vegetation by reference to Smuts, Spencer and Henderson, that does not necessarily imply that his political opinions or social goals were the same as any of theirs. He may well have claimed kinship with the many different contemporary forms of holism simply to enhance the credibility of his own conception of the natural community. One need not, for instance, regard Clements as necessarily sharing Henderson's Harvard conservatism.[243] Furthermore, although it is clear that he had interests in common with the Chicago animal ecology group, and agreed with them on the importance of the organismic analogy, his views were not necessarily completely identical with theirs. One need not imagine that Clements shared, for example, Allee's Quaker beliefs in social altruism.[244] The concept of society as a social organism may be applied in many different ways. Indeed it is important to note that there is a systematic difference in the political moral drawn from the organismic analogy by Clements as compared to Spencer. In Spencer's work, the organismic nature of society implied that efforts by reformers and planners to change the social structure or control economic competition could only damage the highly organised social organism.[245] To Clements, however, the organismic analogy guaranteed an active role for the expert in social planning.[246] Only an expert could comprehend and guide the intricate working of holistic systems.

Hofstadter has described the vogue for Spencer which gripped the farming communities of the American Middle West at the turn of the century. Spencer was the "shining light of individualism".[247] A whole generation was brought up on "Republicanism, Presbyterianism and Spencerianism".[248] Thus, Clements cleverly adopted an idea in common currency among his lay constituency and adapted it to serve his own, somewhat different, purposes.

As well as his explicit references to holist theorists like Spencer, there were further resonances between Clements's discourse and the political discourse of his lay constituency - most importantly with the rhetoric of the Populists. Populism was a political movement engendered by the agricultural discontent of the eighteen eighties and nineties.[249] It was particularly strong in Nebraska in the 1890s. Hofstadter has identified the idea of a natural harmony as being a dominant theme in the ideology of the Populist movement:-

> "In assuming a lush natural order whose workings were being deranged by human laws, Populist writers were again drawing on the Jacksonian tradition, whose spokesmen also had pleaded for a proper obedience to "natural laws" as a prerequisite of social justice."[250]

Thus a contrast between harmonious nature and disruptive Man was not an element which Clements introduced into the political discourse of the Middle West.[251] However, in adopting this well-known argumentative resource, Clements changed its implication so that the harmony of nature no longer predicated Jacksonian individualism but rather collectivism and technocracy. It was the individualistic actions of the homesteaders that were deranging nature, not Eastern legislators as the rhetoric of Populism had claimed. A proper obedience to 'natural laws' was indeed a prerequisite of social justice, but science had demonstrated that the laws of nature were ultimately those of cooperation and integration.

Cooperation was a natural characteristic ('function' in Clementsian terms) of all organised communities. It would grow spontaneously within the farming community of the Plains as a reaction to environmental stresses to which the community was being exposed. The role of the expert was to guide and direct the new expression of cooperative spirit:-

> "Coordination of process and practice on farm or ranch must be reflected in the organization of the community. This signifies cooperation, a community function still almost undeveloped except with respect to marketing. Though by far the most important of social processes, it has made such slight progress against myopic individualism as to confirm the belief that, like the functions of other and simpler organisms, it can be evolved only under the stimulus of outside forces. Fortunately, times of stress provide the very pressure needed as well as the agencies to guide the response to it, and it now seems probable that cooperation will be set forward more in the present generation than in the full century since the settlement of the West began."[252]

As we have seen, Clements sought to establish a role for central technical authority in an area previously given over to the free interplay of individual and interest-group advantage. He advocated federal intervention in many aspects of land use - in a society where such intervention had previously been anathema.[253] He sought to limit the freedom of the homesteader to settle on marginal land - a policy which would entail that the expansion of the agricultural yeomanry was finally over and would make the High Plains the preserve of the ideologically unpopular cattleman.[254] But Clements sought to direct the rancher too - with a leasing system for the Public Domain which would entail strict federal controls over stocking levels, irrigation and all land utilisations, and which would yield revenue for the federal purse. In all these difficult tasks the image of a harmonious, organismic natural order was a powerful tool - functioning to persuade the relevant parties that there was a welfare to be served greater than that of the individual or particular interest-group:-

> "What has been said of farm and community applies with like force to every social integration of higher rank and especially to the nation as a whole at a time when it has delegated powers to a degree hitherto unknown. Within such a huge organism, the whole is much greater than the mere sum of its parts, and hence the need for coordination and correlation far transcends all other considerations whatsoever. It is here that cooperation will meet its supreme test and it can emerge from this successfully only as the ecological ideal of 'wholeness' or organs working in unison within a great organism, prevails over partial and partisan viewpoints."[255]

Another ecologist who drew the same moral as Clements from characteristics of the biotic community was W.P. Taylor. Taylor was Senior Biologist with the U.S. Biological Survey, based, in the early thirties, at Tucson, Arizona. Given his position with a Government agency, it is not surprising that he expressed a belief in the potentialities of ecology as an applied science. To Taylor the applicability of ecology was, in principle, endless. Not only could ecologists hope to advise on all matters associated with agriculture, soil erosion control, land use classification, re-settlement, fisheries management, water resources management, reforestation and range rehabilitation, an even more noble enterprise beckoned them:-

> "What, after all, is more reasonable than the ecological approach to anthropology,economics, sociology and ethics? Man's evolution, development and behaviour are inevitably so closely related to his environment that the ecological viewpoint seems the most natural in the world."[256]

Taylor was eager to grasp the opportunities for ecology offered by the New Deal:-

> "The program of President Franklin D. Roosevelt and the Congress of the United States (spring 1933) to give work to 250,000 of the unemployed in reforestation affords an opportunity, perhaps of its kind unparalleled in the world's history, for application of ecological information."[257]

His rhetorical repertoire was strikingly similar to Clements:-

> "The farm is properly an ecological enterprise. The ideally diversified farm is one on which there has been set up an artificial but well-balanced biotic community ...The less well-balanced the biotic community on the farm, the more precarious its economic future ... What is so obviously true of the farm is equally true of science and administration of natural resources as a whole, in America and the world over. Just as the farmer's present and future prosperity depends on science, intelligence, cooperation in ever-larger units, and a well-balanced biological enterprise on his land, so the welfare of the human race depends on science, intelligence, breadth of view, cooperation in ever-larger units, scientifically and administratively, and a well-balanced maintenance, development and use of world natural resources."[258]

Cooperation, whether on the farm or on Capitol Hill, was the best human policy because it was the most natural one:-

> "Apparently there is little rugged individualism in nature ... the biotic community, the interacting, interrelated, interdependent, loosely or closely organized cooperative commonwealth of plants and animals in their environments, is more nearly an organism than the sum of its parts."[259]

The lack of rugged individualism in nature had direct consequences for human action:-

> "The stockmen themselves are slowly but surely coming to realize that unregulated competition for private profits and proper care of the land and its resources simply do not go together."[260]

We see therefore in Taylor, as in Clements, that the image of a cooperative community of plants and animals functioned as a legitimation of the role of the ecologist as an expert adviser and director of human activities. However in Taylor's hands the organismic analogy displays further subtleties of persuasive potential. Firstly, as well as legitimating the role of the expert to the layman, it also may be used to enhance the status of the ecological expert as against his technocratic peers and rivals. Other experts, conditioned by their specialist education, may take only partial viewpoints - only the ecologist has the professional capability of accurately perceiving the holistic unity of nature:-

> "The man who is sick and in need of medical attention needs a physician who can see his difficulties as a whole. It is disturbing to consult two or three specialists in as many different organs of the body and to be given a regimen for the improvement of each which cannot possibly be carried out in view of what has been prescribed already for others. Some master practitioner must harmonize the various proposed cures or the sufferer is heading for difficulty.
>
> I like to think of ecology as a sort of master diagnostician who tries not to lose sight of the fact that Nature, the patient, is not an accidental collocation of independent and unrelated objects, but is normally an organized and functioning whole."[261]

Secondly, the image of an organic natural order could be used to persuade the layman not to expect too much too quickly from his scientific adviser. It provided a defence against failure to fulfil expectation. The scientist too was constrained by nature - healing the biotic organism could only proceed at nature's own pace:-

> "The faith of some of the farmers and business men in science and scientific men is almost pathetic. Many seem to believe that various artificial measures, erosion control, reseeding, replanting, weed control, rodent control, or other measures will suffice to repair the obvious damage, even in the absence of removal of the over-heavy pressure from livestock which in the case of the grazing range is the fundamental and continuing cause of many of the difficulties ... Formulas for the quickest repair of the damage done are now being sought by engineers in cooperation with ecologists. Who better than the ecologist, after all, can be counted on to see clearly through the processes which have been going on, to picture accurately the land as it ought to look and to advise safely what should be done?"[262]

The best evidence we have that Clements's organismic metaphor functioned as a persuasive device is that it was so perceived by his contemporaries, indeed was so perceived by the people he was attempting to persuade. James Malin, for example, was a historian at the University of Kansas who sought to counter the claims of the technocrats and oppose the collectivist tendencies of the New Deal. Born and reared on a family farm, he took it upon himself to champion the culture and defend the individualistic prerogatives of the Plains dwellers.[263] Malin identified Clementsianism as posing a threat to the Plains community because the implication of Clements's ecological arguments was that relatively narrow natural limits were placed upon the activities of the farmer on the Plains. Furthermore, the threat of Clementsianism was a serious one because Clements's ideas "became entrenched in the United States Department of Agriculture".[264] The U.S.D.A. provided expert advisers who sought to specify which farming techniques ought to be applied on the Great Plains.

Malin had a low opinion of most advisory experts, who in their scientific arrogance "not only disregarded, but ridiculed, folk knowledge".[265] Malin questioned the universal utility of applied science in agriculture:-

> "The difference between folk knowledge and scientifically determined applications of knowledge became more

sharply drawn, but not always to the credit of science."[266]

Malin regarded the scientists and funding agencies eager to apply science to the practical problems of the mid-continental area as carpetbaggers:-

> "A large part of American research funds and energy is expended upon technological research of a short-term character to achieve functional ends, often primarily for political advantage ... Government funds, foundation funds, university funds, poured out to any Johnny-come-lately for 'quickie research' cannot meet the challenge."[267]

Malin categorised Clements as a "closed-space" theorist - one who regarded the potentialities of man and nature to be finite and definable.[268] This was a characteristic Clements was held to share with another bête noire of Malin - Frederick Jackson Turner. Turner had argued that the existence of the frontier and free land had shaped American society - creating a democratic, individualistic and egalitarian society.[269] But the Turnerites had further argued that the disappearance of the frontier had irrevocably changed the nature of American society. With the frontier gone, democracy could no longer depend on individualism - it must be collectively sustained.[270]

Malin, on the other hand, maintained that in fact the relationship between Man and Nature was an open system. Its potentialities were infinite:-

> "There can be no such thing as the exhaustion of the natural resources of any area of the earth unless positive proof can be adduced that no possible technological "discovery" can ever bring to the horizon of utilization any remaining property of area ... Historical experience points to an indeterminate release to man of such "new resources" as he becomes technologically capable of their utilization. At one stroke, such a concept renders the Turner-Mackinder doctrine of closed space meaningless and correspondingly destroys the basis of the argument of the "closed space corollary to the Turner frontier hypothesis" which held that a welfare state - a regimental social order must be instituted to serve as a substitute for the "closed frontier" in order to preserve American democracy and opportunity."[271]

The frontier was endless.

To Malin, there was no such thing as a natural balance or harmonious state of nature on the Plain which modern technological man had disturbed. The stable climax of which Clements spoke was a "state of mythic equilibrium":-[272]

> "How can the idealized type of theoretical climax, either of soil or of vegetation, have culminated under the conditions of continuous disturbance established by history ... the concept of climax must be redefined, especially ... its time requirement, both as respects soil maturity (climax) and vegetational climax. Furthermore, in that case, the implication that vegetational succession and climax are dependent upon progressive soil changes in the direction of maturity needs restatement or abandonment."[273]

Malin argued, using historical and archaeological evidence, that there had been soil loss from the plains grassland, and even dust storms, before the sod was broken by the steel plough. He maintained that being overgrazed was likewise the natural condition of the plains due to the vast herds of bison that had roamed there before the arrival of the white man. The Indians had also had considerable perturbing impact upon the vegetation.[274] Therefore "the plow that broke the plains" was not guilty.[275] The homesteader had not been the unique agent of disturbance the conservationists claimed. Rather the impact of European man on the plains had been simply one further chapter in a story of endless indeterminate change and adjustment.

Malin acknowledged that many of man's activities were in actuality often circumscribed and controlled by characteristics of the natural environment. But <u>potentially</u> the relations between Man and Nature were infinitely flexible. The "contriving brain and the skilful hand"[276] were ever exploiting new resources, solving old problems, overcoming natural barriers. To hold that the expanding era of the homesteader was over was to impugn the farmers' native resourcefulness and invention, and to misunderstand the essential open-endedness of Man's interaction with Nature.

Clements's closed-system organismic conception of nature was scientifically defunct:-

> "In all the discussion by the biologists of organism, environmentalism, and managed society, there was a

conspicuous absence of historical perspective. Organism appeared to them to be a discovery arising out of the ecological approach to the study of plants and animals, when in fact the concept was already quite fully developed in Plato's time. The historian of political theory had given it most careful attention, because it was a favourite concept used in justification of absolute monarchy and arbitrary power in early modern times. The democratic tradition had challenged the idea that the king was the directing brain of the political organism. The standard textbook in principles of political science written during the progressive era before World War I identified the concept of organism as the bulwark of the authoritarian state, and treated both as discredited and discarded concepts. It seemed scarcely necessary at that time to devote such space to performing post-mortems."[277]

The organismic concept of nature had no validity and served only the interests of authoritarian 'experts':-

"It is evident that in the twentieth century several patterns of thought were taking shape, apparently independently of each other at first, but after World War I with increasing interaction. Among them was the myth of the inevitability and necessity for regimented organisation and management of society. The ideas of organism and environmentalism in the biological and social sciences were an integral part of the pseudo-scientific process of rationalizing the myth. It was a natural outgrowth of an age that had come to worship science, the marvels of the laboratory, and their applications by the engineer, and that, in consequence, became obsessed with the conviction that human affairs could be managed similarly."[278]

Organicism formed part of a general threat to American individualism and democracy - a threat exemplified by the 'socialism' of the New Deal.[279] Like all forms of collectivism, organicism was totalitarian and "denied the validity of the individual".[280] It represented an attack on the freedom of the citizen:-

"If the organismic idea was carried out to its logical conclusion then each human being in the social organism was comparable to the cell in the plant or animal body and the capacity of the common man to manage his own affairs was denied. Instead of a defense of equalitarianism, the organismic idea was a repudiation. The assumption was that the expert, the "brains trust", <u>e.g.</u>, the superior people, were alone entitled to manage the affairs of society."[281]

The dispute between Clements and Malin mirrors a long-standing dichotomy in American political debate. Malin drew upon the long tradition of American individualistic social thought - a conception of society which put the individual and only the individual in pride of place. The occurrence of such ideas in American political rhetoric dates from the time of Jefferson, if not before.[282] Individualism had, since Jefferson's time, been invoked in many different ways, harnessed to a wide variety of political ends. Malin was thus utilising old styles of argument, powerfully resonant with implication, and recasting them to serve his own purposes. But dominant though individualistic rhetoric has been in the history of American political thought, there has always existed the alternative rhetorical possibility of emphasising the prerogatives and obligations of the State, and the individual's responsibility towards his fellows - of answering individualism with centralism or collectivism of one variety or another. Clements, like Malin, was invoking already existing forms of argument and utilising them for his own purposes. The rhetorical strategy, chosen by the technocrats in general and Clements in particular, cannot therefore be fully understood unless this background of an enduring pattern of ordering and re-ordering the same or similar polemical resources is borne in mind.

Sigma school - a technical context of classification

To the Sigmatists the vegetation unit was not an organism. The association was regarded as a real but abstract category of which the individual stands were representative and into which they were to be grouped by the classifier.

It is not so much that Braun-Blanquet disagreed with Clements's organismic theories but rather that such discussions were irrelevant to his purposes and meaningless within his social and political context. Braun-Blanquet worked within quite a different tradition of social thought from that which impinged upon Clements. In as centrally organised a country as France, the principle of State intervention in the area of land-use legislation, did not have to be argued for.[283]

French ideology of statecraft had never enshrined rugged individualism in the American manner. Debate over the true nature of the French state had flowed in other more collectively-oriented directions.[284] Both the conservation and the technocratic movements came late to France.[285] The phytosociologists did not have the opportunity to aspire toward becoming environmental technocrats in the manner of the American ecologists. Thus Braun-Blanquet, interested though he was, to an extent, in presenting phytosociology as applicable, was clearly not in a position equivalent to the American technocrats with their professional mission to slay the dragons of frontier individualism and robber-baron laissez-faire.

In contrast to the position in Nebraska, in Montpelier the nature of the plant community was purely a technical matter. Discussion as to its character occurred only between accredited members of the specialty. There was no French equivalent of James Malin. The nature of the plant association did not function as a polemic resource in a wider realm of social suasion. Thus, it is understandable that the Sigmatists' conceptualisation of the nature of their basic unit was similar to that found in taxonomy - the model from which the form of phytosociological classification and many other elements of their practice were derived.

Incommensurability

Having traced the divergence and separate development of the Clementsian and the Zurich-Montpelier systems, we may note that they existed as quite independent representations of nature. Each was a harmoniously interrelated network of observation, theory, classification and application. Each system embodied its own form of scientific practice. There was no possibility of independent arbitration by Man or Nature as to the validity of the two forms of ecological knowledge. The Clementsian and the Zurich-Montpelier systems were, in a word, incommensurable.[286]

Incommensurability was not the product of ignorance or lack of understanding. The Sigmatists followed American work closely, admired some of it and understood the purpose of the American procedures. But they regarded American data as irrelevant to their own phytosociological purposes. The differences of opinion over the characterisation of the fundamental unit serve to illustrate this. To the Sigmatists, floristic characterisation of vegetation units was a key point of classificatory procedure. The making of association tables and lists of characteristic species composition were essential steps toward deciding if any given vegetation unit was valid. The Americans did not use these procedures. (It would have been very difficult for them to do because their units were so large). How, then, could the Sigmatists decide if the American units were valid or not? Braun-Blanquet outlined the problem:-

> "It [the American association] is ... very poorly circumscribed, a fact which may perhaps explain why no American botanist has given a detailed tabular analysis of a single association. This unit is large and difficult to grasp ... Any unit corresponding to our association is lacking. The "consociations" ... of Clements and Weaver are based entirely upon the dominance of certain species; they are thus quite incapable of replacing our association in any system of classification ... In an excellent paper, which may be considered a model of the Clements-Weaver school, Steiger ... has given a careful quantitative floristic and ecological study of a portion of the prairies. These valuable ecological data cannot, however, serve to individualize the sociological unit. This seems to furnish the best proof that the most exact ecological data remain sterile for sociological evaluations when assembled according to the system of Clements and Weaver."[287]

To Clements, on the other hand, the very smallness of the European units rendered them irrelevant to his purposes. Furthermore, the European units were not characterised developmentally. The European association was not necessarily a climax unit. But since, to Clements, vegetation was dynamic and progressive, nothing else but a climax unit could furnish a reliable basis for classification. Successional vegetation was transient and did not display a full expression of the habitat in the way that climax vegetation did. Also, the modified vegetation of Europe could not be taken as a reliable guide to natural conditions. American vegetation was more natural and therefore a better basis for the construction of classification systems:-

"The major difficulty in the analysis of vegetation is its great complexity, but it discloses a definite pattern when analyzed from the developmental point of view. The study of a local area of vegetation should always be supplemented so far as is feasible by examining that of adjacent regions ... Moreover, all ecological investigators have not given the same rank to equivalent units of vegetation. This has resulted often from the limited area studied, i.e., its relations to adjacent major units were not determined, or sometimes from the fact that the studies were made in transitional areas. Moreover, in countries long occupied by civilised man, the natural vegetation is represented by the merest fragments."[288]

The Sigmatists acknowledged the importance of investigating plant succession, but did not accord its study the primacy Clements did. Moreover, they considered their own vegetation an adequate basis for ecological classification:-

"[Clements's] dynamics are often hypothetical, and the static social units are indispensable as a foundation for any study of vegetation ... It must not be forgotten ... that the areas today occupied by climax stages have become greatly reduced ... The developmental stages, on the contrary, still occupy immense areas. It seems therefore unfortunate to burden terminology with the introduction of special terms to distinguish stages which appear to be climax and stages which are developmental."[289]

Thus each side rejected what the other regarded as the essential principle on which ecological classification should be built. The Sigmatists did not acknowledge the primacy of development, nor the necessity of basing ecological precepts upon the study of large expanses of undisturbed vegetation. Clements did not acknowledge the primacy of floristics, nor the suitability of European vegetation as a basis for ecological theorising. Neither side could meaningfully engage with the other as far as the practical elucidation of ecological fundamentals was concerned. Furthermore, both sides would have rejected the idea that random sampling of vegetation could arbitrate and display what the natural units really were.[290] Random sampling would not be reliable since it would necessarily include disturbed, heterogeneous or transitional stands. Each system could only be judged by criteria internal to itself.

Conclusions

In the previous chapter we saw how the idea of the plant community, the idea that there were natural kinds of vegetation, arose with Alexander von Humboldt and his immediate followers. We saw the development of a Humboldtian tradition of plant geography which employed such a unit. In the present chapter we have seen that both Clements and Braun-Blanquet had a large intellectual debt to that tradition. Their early work was done in relation to it. Yet they were quite different from Humboldt in cognitive interests and in conceptualisation of the form of the natural unit. In these respects they are also quite different from each other. It would be hard therefore to claim that the history of the plant association from Humboldt to Clements was the history of a unit-idea, since it seems difficult to claim that Clements's conceptualisation of the plant association was, in any way, fundamentally or essentially the same as Humboldt's. One of the purposes of this chapter is to display the inherent flexibility, the malleability, of the notion that vegetation occurs in natural units.

It is certain, however protean the research tradition was, that there was a real historical connection between the activities of Humboldt on the one hand, and Clements and Braun-Blanquet on the other. But what I have tried to present in these first two chapters is not the history of a unit-idea, nor a unitary tradition of practice, but an account of how, as men find themselves in new contexts which bring new challenges and new demands, the ideas they have inherited from their predecessors function as resources to be changed, refurbished and re-made to serve new purposes.

This is not to say that ideas are epiphenomenal. To Clements and Braun-Blanquet the Humboldtian idea of a natural unit of vegetation was an important resource. And they employed their own conceptualisation of the natural unit to do important tasks. As we shall see in the following chapter, those of their successors who sought to redirect the discipline of ecology and reform its practice, felt obliged to engage Clements at the level of ideas - to challenge his conception of what the underlying nature of the plant community was.

I have also sought to display how the Clementsian and the Sigmatist conceptions of the plant community were not, either of them, wholly determined by Nature itself. I have sought rather to indicate how ideas of the plant community are conventional in that they are constructed within social contexts and structured by social purposes both internal and external to communities of trained scientists. I have also sought to show how scientific views of nature may intermesh with networks of usage beyond the purely technical. To put it plainly, ideas of nature are part of culture. There are important differences between American and French culture, even scientific culture. Therefore different forms of knowledge about nature are produced in the different countries.

Maintaining this is not, however, to detract from the status of the Braun-Blanquet and Clementsian systems as carefully observed and technically successful representations of Nature. It is clearly within the ingenuity of Man to produce theories which fulfil many purposes at once.

CHAPTER THREE

HENRY ALLAN GLEASON
AND THE INDIVIDUALISTIC HYPOTHESIS

Introduction

Clements never quite achieved the recognition which he so obviously sought and which he thought his due. He was certainly the major theorist of early twentieth-century American ecology.[1] He published several times more text, many more books, than his nearest rival. Much of what he wrote exerted considerable influence on how American ecologists described vegetation. It cannot be denied that he was acknowledged by his contemporaries to be an important figure within the field of ecology. Yet, strangely, he seemed also always marginal to it.[2]

Clements had a strong coterie of followers, in the West and Middle West. He often collaborated with John Weaver, Professor of Botany at the University of Nebraska. Weaver had been a graduate student under Clements in Minnesota,and throughout his working life he shared Clements's concern with the management of the plains and prairie grasslands. Clements also appears to have received much support from among the practical men of the State and Federal advisory agencies.[3] Yet at no time could it be said that the majority of American academic ecologists were unreservedly or wholeheartedly Clementsian. Clements, it might be said, seemed like a hero who pitched his tent apart.

There were a variety of reasons for this. Clements's writings, while admirably comprehensive, were prolix and too often seemed grandiosely speculative or inflexibly deductive. His fellow ecologists, despite having adopted much of his terminology, cavilled at what they chose to regard as his over-elaborate neologisms and unduly rigid and *a priori* definitions.[4] Personally Clements often seemed intellectually arrogant, aloof and unclubbable.[5] He was, all in all, not a charismatic leader. It is significant that he never held a senior position in the Ecological Society of America although he was a charter member when the society was founded in 1914.[6] His health was never altogether robust and in later years, he seldom attended botanical meetings.[7] He rarely replied to, or even acknowledged, criticisms of his work - concentrating instead on developing and articulating his own system.[8] Joining the Carnegie Institution in 1917, although he continued for many years afterwards to teach summer schools for the University of Nebraska, Clements cut himself off from the vital life-line of graduate students.

Thus, in the nineteen-twenties and -thirties, pedagogical pre-eminence within the newly emerged discipline of American ecology fell to H.C. Cowles at Chicago, W.S. Cooper at Minnesota, and G.E. Nichols at Yale. Their institutions were the principal centres at which the next generation of ecologists were trained, and, correspondingly, the importance of their intellectual leadership was considerable.[9]

As I have stressed in the previous chapter, the need to communicate directly with a lay audience exercised a considerable influence on Clements's work. In the Land-Grant Colleges, in which context Clements formulated his research programme, scientific research, of whatever sort, had to appear readily applicable. But at universities such as Chicago and Yale, for example, the need to appeal to a lay constituency was less acute. There was more institutional support for pure research than was ever possible at Nebraska or Minnesota.[10] While ecologists, wherever in America they were based, were unlikely to neglect altogether the claim that ecology was an applicable subject, outwith the Land-Grant Colleges more traditional notions of the scope and content of botany held sway. This variety of institutional settings meant that not all ecologists were surrounded by quite the same constraints as Clements was, and thus they had the possibility of fostering alternative points of view.

But, despite considerable disagreements on other matters, American ecologists concurred with Clements almost to a man - Cowles, Cooper and Nichols included - that vegetation existed in real natural units which had an individuality of their own. The one man in the whole of America who openly and explicitly dissented from Clements's view on this point, between 1917 and 1945, was Henry Allan Gleason, the champion of an alternative 'individualistic concept' of the plant association. In 1917 and again in 1926, Gleason argued that the association was "not an organism, scarcely even a vegetational unit, but merely a coincidence."[11] Gleason acknowledged that one could identify, in the field, areas of vegetation which exhibited uniform floristic composition over appreciable areas. In this concrete sense definite associations existed. But the phenomena of the plant community depended entirely, Gleason argued, upon the behaviour of individual plants. Thus, associations did not represent basic units of which all vegetation was comprised. In any sense other than that of a concrete stand of plants, the association concept was a classifier's category, sustained by the activity of classification rather than by the reality of vegetation:-

> "Different mills produce different qualities of flour from the same wheat. The association concept is the product of our mental mills."[12]

Gleason did not remain an ecologist throughout his entire career. While comparatively young, he progressively abandoned ecological work to devote most of his research energies to what had always been the other string to his bow - taxonomy. Working within the splendid facilities of the New York Botanical Garden, he established himself as one of America's leading systematic botanists.[13] He was continuously productive and innovative within taxonomy for more than sixty years. But he was, in the twilight of his career, called back into ecological debate - to be acclaimed as the lost founding father of plant ecology, the clear-sighted pioneer whose counsel the discipline had neglected for forty years, to its serious detriment. His early publications were re-examined. His individualistic hypothesis was revived. He was made the patron and the figure-head of the discipline's post-war transformation.

Gleason is thus a figure of considerable interest in the history of ecology. Yet no full account of his life and work exists.[14] The first purpose of this chapter is to remedy this neglect of

Gleason by providing a comprehensive account of his career in ecology. My treatment of Gleason will be chronological. I shall follow the development of his career from its beginnings - examining his ecological researches and publications one by one. Within this framework I shall trace the development of Gleason's views as to the nature of the plant association and elucidate the reasons behind his radical dissent from generally received opinion on the question of natural kinds of vegetation. I shall describe how Gleason's career was shaped by a variety of social, personal, scientific and extra-scientific factors. I shall also examine why the Gleasonian individualistic concept of the plant community was so comprehensively rejected by his American contemporaries when it first appeared. The eventual general acceptance of the individualistic hypothesis is considered only very briefly in the present chapter, but is more fully described in Chapter Four.

As well as providing essential background to the debate over the nature of the plant community, Gleason's career in ecology is of more general interest. The period of his maximal involvement in ecology was also the period during which ecology became institutionalised as an academic discipline in the United States.[15] I shall argue that Gleason was more centrally involved in early American ecological activity than recent commentators have given him credit for. I hope that elucidation of Gleason's work within ecology will shed light not only upon the individualistic hypothesis, but upon the research practices and intellectual concerns of ecology as a whole in these formative years. In particular, it will highlight how cognitive innovation in the new discipline was structured around the prior professional commitments and skills of its recruits from other disciplines.

Unfortunately I have been able to pay little attention to Gleason's work in taxonomy, save where his taxonomic and floristic concerns have implications for his ecology. It is important, however, to bear in mind that this is Hamlet without the Prince of Denmark. Considered over the course of his whole career Gleason was, quantitatively speaking, much more of a taxonomist than an ecologist.[16] The present essay, concentrating as it does on his career in ecology, is far from being a balanced account of his scientific career as a whole.[17] While efforts are made throughout to acknowledge and allow for this larger undescribed aspect of Gleason's professional activities, the reader must often balance these matters for himself.

Early botanical training

Henry Allan Gleason was born on the 2nd January 1882, on a farm near Dalton City, Illinois. In 1892 the family moved into the town of Decatur, Illinois. Gleason reacted against the strange urban environment by taking an interest in the outdoors:-

> "As a small boy, brought up on a farm with no other boys near by, I had never learned how to get along easily and smoothly with youngsters of my own age. After my parents moved into a good-sized town when I was nearly eleven years old, I was involved in a continuous warfare with other boys. Living at the edge of the city, with woods and a river just a short distance away, I turned to the woods for recreation."[18]

At the High School in Decatur, Gleason acquired his first formal instruction in botany and natural history. However, important though the school tasks of collecting and naming flowers undoubtedly were in stimulating Gleason's early botanising, he was largely self-directed. And, equipped with Gray's Manual and a home-made plant press (both presents from his father who greatly encouraged his interest in natural history) he was a precocious naturalist. In his autobiography, he recorded his surprise, on re-reading his boyhood notebooks, at the accuracy of his identification of species and the care with which he had made his notes.[19] This capacity for careful attention to detail was to provide the foundation for Gleason's rapid acquirement of important botanical skills.

By the time of his graduation from high school, Gleason had determined to become a professional botanist and he had already laid the foundations of his future competence:-

> "Three years of collecting had taught me how to make specimens and identify them, had given me a fair-sized collection of my own, probably two or three hundred sheets, and had still further increased my love for wild things and for the fields and woods where they lived. I was now fully decided to be a botanist, not because of any instruction I had received or for any promises made to me for the future, but simply because I liked plants."[20]

In the autumn of 1897, at the age of fifteen, Gleason entered the University of Illinois. In his first year, he registered for an elementary course in entomology.[21] This course was remarkable, indeed probably unique for its time, in that it was taught by two men who were later to achieve recognition as pioneers of ecology in America. Stephen A. Forbes gave the lectures. Charles C. Adams was the assistant in charge of the laboratory classes. Both of these men were to be early presidents of the Ecological Society of America, Forbes in 1921 and Adams in 1923.[22] Adams, who had only recently graduated, left Illinois in 1898 to do graduate work at Harvard.[23] Detailed discussion of his association with Gleason will be left until later.

Forbes, on the other hand, was already by this time a well-known biologist.[24] As well as his post at the university, he held the directorship of the State Laboratory for Natural History through which he supervised the state-funded programme of research into economic entomology and limnology. Forbes was one of a quartet of eminent biology professors, all located in the Middle West, who were present at the birth of ecology in America. The other members of this foursome were S.M. Coulter, teacher of H.C. Cowles at the University of Chicago, E.A. Birge at Wisconsin and C.E. Bessey at Nebraska. These men, although not themselves trained as ecologists, all became interested in the new science, cultivated it, and were influential in the careers of many of those members of the next generation of biologists who were to establish ecology in America.[25] Forbes was himself very active in ecological research. Indeed at the turn of the century, he was probably the leading student of animal ecology in America.[26]

One of Forbes's principal research interests was the interrelations between organisms, particularly between predator and prey species. He held that natural selection worked not entirely in the individualistic Darwinian mode but also upon groups, thus producing stable balanced assemblages of species. Entire complexes of species were said to have a 'community of interest'.[27] As early as 1880, Forbes had developed a concept of the 'biotic community' - which was later acknowledged by Clements to be very similar to his own, lacking only the distinctively Clementsian emphasis on developmental change.[28] Forbes's study of ecological inter-relations between species was also innovative in that it was often quantitative. He devised a 'coefficient of association' to aid in statistical analysis of the mutual occurrence of species.[29] Although famous principally for his work as a zoologist, Forbes was also an accomplished field botanist and had made valuable contributions to the knowledge of the Illinois flora.[30] Thus, on becoming a student at Illinois, Gleason had entered one of the very few institutions in the United States in which, prior to the end of the nineteenth century, ecological ideas were being taken seriously and ecological practice was being nurtured. And he had made personal contact with one of the leading practitioners of a style of field research newly introduced to America - research based upon the identification of communities of organisms.

One of Forbes's assistants in the State Laboratory was the entomologist, Charles A. Hart. Hart was an avid field worker and collector, and he and Gleason were soon close friends:-

> "My first real botanical trip came in the summer of 1900, when C.A. Hart invited me to go with him on a collecting trip to Grand Tower in Southern Illinois. I knew of the wonderful flora growing there ... Hart knew the surface geology of the state and told me about the various stages of glaciation and the moraines, and I believe I got from him at this time my first inkling of such phytogeographical matters."[31]

This was the beginning of a long and fruitful collaboration between the two men. Gleason came to admire Hart greatly and learned a great deal from him. He was to describe on more than one occasion the important role which Hart's knowledge of the areas they studied played in the development of his own ecological ideas. Hart was an entomologist. Gleason's botanical knowledge was already much superior, but Hart:-

> " ... knew the history, geography, geology, physiography, climate and fauna of the state of Illinois with most surprizing thoroughness. A field trip with him was an education in itself."[32]

The nature of Gleason's indebtedness to Hart provides us with an insight into the character of Gleason's first forays into ecology. Indeed it tells us much about the nature of early ecology as a whole. In America, as in Britain, ecology initially sprang from, and was an extension of, the interests and the skills of good field workers from the disciplines of taxonomic botany or zoology. The best taxonomists had always been interested in the "history, geography, geology, physiography, climate and fauna" of the areas in which they searched for specimens. They were natural historians as well as systematists. Much early ecology amounted to an attempt to shift these and other related interests towards the centre-stage of biological inquiry - to formalise into a science an area of knowledge which had previously been informal and auxiliary to taxonomic botany.

The continental model of ecological plant geography seemed to offer a vehicle with which to achieve this. If, as I argued in the previous chapter, ecology was represented by its early practitioners as physiology extended from the laboratory into the natural environment of plants, it was also, in Britain and America, natural history newly re-made in a scientific guise. It promised to provide a new, respectably scientific, context within which botanists, fond of field work, could exercise their traditional skills.[33] As we have seen, Gleason had many of the skills of the natural historian before he arrived at Illinois. Hart developed these skills further, thus equipping Gleason for the new field science of ecology.

It was not long before the ecological orientation of his academic environment began to have its effect on Gleason. Although he majored in botany rather than zoology, he attended several further classes under Forbes and endeavoured to incorporate an ecological perspective into his own work. He began to study plant communities:-

> "For my [B.S.] thesis I took as a subject the flora of the prairies and worked away earnestly on it through my senior year. I tried to compile a list of all the prairie plants of Illinois and to discuss their distributions and associations as best I could. In the latter I did very poorly in comparison with present day standards, for ecology was not developed as it is now. I had a very meager idea of associations and no idea at all of succession."[34]

Learning from Forbes and Hart prepared Gleason for other influences:-

> "Late in my senior year, Cowles' studies on the physiographic ecology of Chicago were published in the Bot. I had paid no attention to his earlier studies on sand dune vegetation, but for some reason this article attracted me. I at once attempted to apply his ideas to conditions in the woods north of Urbana and to my great delight found they apparently held. So his work and my application of it was presented before the Natural History Society, and this was my first venture into ecology."[35]

Gleason was not alone in his adoption of the Cowlesian model. Cowles's early papers on physiographic ecology, published in 1901, were a major influence upon American ecology in the first decades of the twentieth century. The study of successional changes and correlations between topography and vegetation-types had already been introduced into the American ecological repertoire by Conway McMillan in his classic study of the vegetation around the Lake of the Woods.[36] But Cowles produced a new conceptual framework which was to win for successional and topographic studies the pride of place within American ecology which they were to occupy until after the Second World War.[37]

American ecologists were, at the turn of the century, borrowing heavily from the new German textbooks - in particular Schimper's Pflanzengeographie auf physiologische Grundlage and Warming's Lehrbuch der okologischen Pflanzengeographie.[38] Warming's book contained a systematic classification of the plant formations of the globe. Cowles, inspired by this example, set out to classify the vegetation of the countryside surrounding Chicago in the Warming manner.[39] The rationale behind the Warming system was that the water content of the soil was the most important habitat factor - determining which groups of plants grew where, within any given climatic area.[40] Cowles, however, came to believe that, important though water content was, a wider range of habitat factors should be considered. He solved the problem with a brilliant theoretical innovation. He made Warming's principal factor - water content - subordinate to another more fundamental environmental variable - topography. Cowles argued that soil water content was itself a dependent variable, dependent upon the slope and elevation of the terrain:-

"The soil conditions are chiefly determined by the surface geology and the topography. The original character of the soil whether rock, sand, clay or marl depends upon the geological relations. From the vegetational standpoint the topographic relations are commonly much more important, since they condition the presence or absence of drainage and hence cause striking variations in air content and humus."[41]

Thus the explanation for the distribution of vegetation lay within the geomorphological process of base-levelling:-

"Having related the vegetation largely to topography, we must recognize that topography changes, not in a haphazard manner, but according to well-defined laws. The processes of erosion ultimately cause the wearing down of the hills and the filling up of the hollows. These two processes, denudation and deposition, working in harmony produce planation; the inequalities are brought down to a base level ... As a consequence of all these changes, the slopes and soils must change; so too the plant societies, which are replaced in turn by others that are adapted to the new conditions. 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 ... Here then is a classification both genetic and dynamic, a classification which has a place for all possible ecological factors."[42]

As the continental land-mass was gradually approaching the condition of a peneplain, the vegetation was becoming more mesophytic - approaching the most mesophytic plant society possible under the regional climate.[43] Thus an understanding of erosion cycles and the processes of topographical change could give the ecologist insight into changes going on within vegetation and would enable him to interpret and classify vegetation upon a developmental basis.

Cowles had cleverly meshed together the European systems of vegetational classification by habitat factor with the theory of base-levelling being employed by American geographers and geologists such as William M. Davis and Rollin D. Salisbury. Salisbury had taught Cowles geology at Chicago.[44] Cowles, in fact, had begun graduate studies in geology before transferring to botany.[45] As Tansley put it:-

"Cowles's training in geology and his keen, abiding interest in the causation of the physical features of landscapes and their relation to vegetation had a decisive effect on his pioneer work and on the whole of his subsequent teaching and activity."[46]

Cowles called his new approach 'physiographic ecology'.[47] His confidence in its value was well-placed. Physiographic ecology was relatively easy to apply, requiring only an elementary knowledge of geology and geomorphology, such as most botanists already possessed and such as Gleason had lately acquired from Hart. It seemed to remove much of the apparent arbitrariness of the European habitat classifications - in which the shape of the classification seemed to depend upon whichever factor individual ecologists assumed was primary. And it conveyed a powerful sense both of ubiquitous vegetational change and of an underlying predictable regularity within that change. It seemed to uncover the laws of vegetational development. And, perhaps most excitingly of all, it promised a privileged insight into the history of vegetation, for:-

> "In many cases, if not in most, there is a horizontal order of succession at the present time that resembles the vertical [i.e. the temporal] succession of which we now have only the topmost member."[48]

Thus by, for example, walking back from a sandy shore one could see laid out horizontally the development stages of the deciduous forest which was now established upon the stabilised and humus-covered mature sand-dunes, furthest from the water's edge.

Cowles's physiographic exemplar was rapidly applied and articulated into new areas by his students such as H.N. Whitford and E.N. Transeau and, rather later but perhaps most famously, by W.S. Cooper on Isle Royale and at Glacier Bay, Alaska.[49] Clements built upon Cowles's 1901 work when he came, three years later, to devise his own 'dynamic' and developmental theory of vegetation.[50]

The system was taken up by many other workers who, like Clements and Gleason, had no direct pedagogical links with Cowles. Areas in which topographical change was most rapid became especially favoured sites for field study:-

> "Throughout the country, young ecologists, of whom I [Gleason] was one, descended on the dunes, the shores, the marshes and the bogs and presently returned to the laboratories to write voluminous accounts of their observations."[51]

Successional diagrams, illustrating how plant communities superseded one another in the overall trend toward the mesophytic climax, became virtually an indispensable feature of published accounts of vegetation.[52]

Gleason made use of Cowles's work again in the research he undertook for his Master's degree. But before we go on to consider Gleason's early ecological research in more detail, we must note that, in those undergraduate years, Gleason was also being trained in other branches of botany. In particular, we must remember that he was acquiring considerable experience in floristic botany which, coupled with his naturally careful, thorough and patient methods of work, was to make him a most accomplished taxonomist at a relatively early age.

In his sophomore year at Illinois Gleason was offered part-time employment in the university herbarium, sorting, mounting and labelling a large backlog of specimens. He seems to have been the only undergraduate assistant of George P. Clinton, who was in charge of the herbarium. Gleason wrote of Clinton that he "had more influence on me botanically than any other man".[53] Clinton taught Gleason herbarium practice and technique. He also expanded Gleason's botanical horizons from his earlier concentration (typical for an amateur) on those plants with conspicuous flowers to almost the entire macroscopic plant kingdom. Gleason continued to work organising the Illinois herbarium throughout his undergraduate career and for three years after his graduation. He was later to write "It is difficult to imagine any better training for my future work than those ... years of mounting plants."[54] Such experience complemented the skills he had already gained during several years of private collecting.

Gleason's taxonomic experience was further widened by a spell (during the summer vacation of 1901) spent working with the famous botanist William Trelease, Director of the Missouri Botanical Garden in St. Louis. Gleason was evidently a satisfactory employee since Trelease offered him a permanent position, but the attractions of continuing at college were too great.[55]

The fact that Gleason developed taxonomic skills as well as ecological ones is important to our understanding of his career development in two ways. Firstly it means that he had a choice of possible careers within botany. He could either become an ecologist or a taxonomist. And, having specialised in one, he could, by sustaining an active interest in the other, retain the ability to change the principal direction of his career, should the need or opportunity arise. Gleason was to move from being primarily an ecologist to become primarily a taxonomist - in 1918 when he accepted the offer of a post at the New York Botanical Garden. And he contemplated the reverse shift on at least one occasion - in 1929, when he sought to return to university life.[56]

Secondly, his abilities in taxonomy were to play an important role within his ecological practice. The ease with which he could find and recognise species in the field allowed him to undertake floristic analysis in many locations relatively readily. This, coupled with his respect for and commitment to the methods of orthodox taxonomy, was to have important consequences for his conception of vegetation. Gleason's perspective on vegetation was always to be floristic - giving a greater importance to floristic data than did, for instance, the members of the Chicago school who, following Coulter and Cowles, always somewhat deprecated herbarium taxonomy in favour of more avant-garde plant sciences.[57] As I shall argue more fully later, recognition of the importance which Gleason accorded floristics is one of the keys to understanding his espousal of the 'individualistic concept'.

Graduate research

Immediately after his graduation, Gleason was appointed to an assistantship in the Botany Department. He remained in Illinois for three more years - teaching, running the department's small herbarium and working for his Master's degree under Professor Thomas Burrill, the head of the department.[58] Burrill was one of the major powers in American botany at the turn of the century.[59] Although in his seventies and approaching the end of his career he was, like Bessey, a zealous advocate of the New Botany. Trained as a taxonomist and active in taxonomic research throughout his career, he had also become famous as a plant pathologist. [In America, the best advocates of the New Botany were often distinguished practitioners of the Old.] He was one of the first to provide experimental evidence that bacteria cause disease in plants, and he was perhaps the first American teacher of botany to instruct undergraduates in the use of the compound microscope (a distinction also claimed for Bessey). Appropriately, the work Gleason did under Burrill's supervision was within the field branch of the New Botany - ecology.

For his thesis Gleason studied the vegetation of the Ozark Hills in Southern Illinois. The finished thesis bears the strong impression of Cowles's influence. Chapters on geology and topography precede the description of the vegetation itself. A Cowlesian description of the plant societies of the Ozarks takes up the major chapter of the thesis. Gleason identified processes of change going on within the vegetation and related these to topographic trends:-

> "The plant associations in the Ozark region fall naturally into three great groups, the upland societies, the cliff societies, and the flood-plain and swamp societies ... By normal processes of erosion and base-leveling the character of the plant growth on any one area is constantly changing, on[e] society giving way to another better suited to the changing ecological conditions. Thus, as a ravine is eroded back into the uplands, the land formerly occupied by a typical upland forest is replaced by a cliff flora, which in turn gives way to the associations of flood-plain or swamp."[60]

But there are other chapters, other elements in Gleason's account of the Ozark vegetation, which indicate the diversity of his interests. Chapter Six consists of a list of all the species known to occur in Southern Illinois. It is a standard taxonomist's regional flora. And Chapter Seven, entitled "Phytogeography", is concerned primarily with the geography, present and historical, of the region's floras rather than its plant associations. Gleason, utilising the newly-published papers of C.C. Adams on the historical floristic phytogeography of the South-eastern United States,[61] outlined how the Texan and other southern floristic assemblages had migrated into Illinois along the natural highway of the Ozark Uplift. Gleason criticised several ecologists, including Cowles and Schimper, for neglecting the relevance of floristic history to the understanding of the region's vegetation:-

> "In Schimper's already classic work the cause of the forest and prairie of the central and eastern United States is given as the amount and distribution of the rain-fall. No account is taken of the fact that the flora of the prairie is distinctively south-western in its origin, that of the forest southeastern. Yet the character of the plant associations in the two formations is probably due as much to their origin as to the present conditions of rainfall and if the two regions were reversed, the arid portion drawing its vegetation from a southeastern origin, and the humid portion deriving its species from the southwest, the results would be strikingly different from the present actuality."[62]

Gleason's thesis as a whole provides much evidence for the view I have advanced above that his perspective on vegetation was always, in an important sense, floristic. He drew upon his floristic knowledge to enhance his ecology and vice-versa. To this extent, Gleason was never altogether a typical young Cowlesian.

Gleason got his Master's degree in 1904, after which he took up a fellowship under Professor William A. Kellerman at Ohio State University. Gleason's work in Ohio seems to have been almost entirely taxonomic. He revised Kellerman's short book The Spring Flora of Ohio.[63] But in the summer of 1905, he became involved in an enterprise which was to be of major importance in his development as an ecologist.

C.C. Adams was back from Harvard with his doctorate and a reputation already established due to his phytogeographical papers. He was now a full member of the Illinois faculty. He was also to be the leader of the University of Michigan's expedition to Isle Royale in Lake Superior, which was planned for the summer of 1905. Gleason wrote to his friend and former teacher applying for the position of plant ecologist to the expedition. That post was already filled but Adams offered Gleason the position of animal ecologist instead. Gleason, it was intended, should devote his energies to the ecology of the invertebrate fauna, in particular the molluscs and insects, of Isle Royale.[64] As a professionally-trained botanist Gleason was not conspicuously well-qualified for such work - but he had studied invertebrate zoology under Forbes (and Adams) at Illinois and he had made quite extensive collections of insects while an undergraduate. Indeed he had been such a good student of zoology that Professor Kofoid had, in 1901, offered him a job with the Illinois State Laboratory, to do research into plankton zoology but "my interest in botany was so great that I could not accept it".[65] Gleason was a naturalist of broad interests and accomplishments. Thus Gleason became part of an expedition which was to be of historic importance, both for its scientific results and for the fact that it heralded the University of Michigan's long-term involvement in large-scale summer field work.

In his autobiography, Gleason recalled that, throughout the summer of 1905 on Isle Royale, in the interval between periods of field work, he and Adams spent much time discussing ecological matters:-

> "[Ecology] was a new subject in those days and Adams and I were pioneers. Clements' book on Research Methods in Ecology had just been published and we had a copy and that was the basis of much of our argument. Adams and I were the only ones who knew anything about ecology and we were usually on the same side and against Clements."[66]

Unfortunately, in his description of these conversations, Gleason gave no clue as to what were the precise grounds for his disagreement with Clements at this stage. However, he summed up the value of his summer on Isle Royale as follows:-

> "I had gained experience with a new flora and with new types of vegetation. I had added greatly to my knowledge of ecology both through discussion and observation. This fact can be best appreciated by reading the first page of my published report."

This report (completed, with Gleason's customary expedition, by the end of 1905 but not published until 1909) does indeed show Gleason's growing knowledge of ecology and the extent to which he was now capable of doing original research.[68] His 1901 B.S. thesis had, as he admitted, shown little understanding of the idea of the plant association and none at all of succession. His M.S. thesis, although bearing evidence of great aptitude for field-work, had been quite derivative, leaning heavily on Cowles's papers on physiographic ecology and Adams's on phytogeography. But in the meantime, successional ideas had become fixed in the minds of all American ecologists by the work of Cowles on 'physiographic ecology' and by their subsequent development and theoretical embellishment by Clements. Gleason had matured into an independent investigator and thinker.

In his interpretation of his Isle Royale invertebrate material, Gleason broadly followed the example of Cowles's work on the vegetation of the sand-dunes of southern Lake Michigan. Gleason was later to claim, justly as far as I am aware, that his 1909 paper was the first to introduce into animal ecology the idea of successional change which had "already been tested pretty thoroughly by the plant ecologists".[69] Gleason, on moving from botany to zoology (albeit briefly) applied his botanical skills and techniques to zoological material.

However, while Gleason can indeed be seen as articulating the Cowlesian exemplar into a new field, he is far from being an unreflective or uncritical follower of Cowles's or Clements's original usages. Clements had followed Cowles by proposing that the present-day climax formations had, at least over part of their area, developed from pioneer associes through a series of stages corresponding closely to those associes which now stand spatially intermediate between pioneer and climax vegetation.[70] Gleason pointedly dissented from these authors' opinions on several matters - most importantly from the assumption that the horizontal zonation of vegetation, such as might occur around the shores of a lake or an island, necessarily represented the chronological sequence of vegetational development which had brought into being the mesophytic vegetation type now found at the end of the horizontal series:-

> "Or briefly, as some ecologists have expressed it, the lateral distribution in space recapitulates the vertical distribution in time. Such an assumption is evidently closely akin to the recapitulation theory of the evolutionists, and ... just as that so-called biogenetic law has been accredited with more than its true value, so has the ecological dictum possibly much less importance than has been usually supposed. The weakness lies in too little consideration of the time element."[71]

To Gleason the theory of vegetational recapitulation could only be upheld if dubious assumptions were made as to the uniformity of climate and constancy of species composition throughout the entire duration of the development of the climax vegetation - that is, if the factors of climatic change and floral migration were ignored. But climatic change and floral migration were key explanatory elements in theories of historical phytogeography. Gleason wished to exploit the potential of Cowles's physiographic paradigm, but he also wished to do historical phytogeography in the manner introduced to America by Adams. There were obstacles in the way of a smooth combination of the two - no historical phytogeographer could afford to neglect the effects of climatic change. Gleason was thus led to criticise a line of reasoning that had caught the imagination of the plant ecologists of his day and launched a thousand field notebooks - the idea that the study of present-day succession gave the ecologist a privileged insight into both the future and the past of any given piece of vegetation. Gleason acknowledged the fascination of interpreting vegetational history, but he cautioned that present-day successions could not be reliably extrapolated very far in either direction. To allow for climatic change, the insights of floristic phytogeography were required. This criticism of successional theory introduced a theme to which Gleason was to return many times in later ecological work. As he expressed it, more than thirty years later:-

> "The former [distribution in space] may be a portrayal of the latter [distribution in time] but not necessarily so, and the further back in time the origin of the "climax" lies, the less is the possibility that modern zonation is a picture of ancient development. In simple words, can you, by visiting the pioneers of Wyoming see how the Puritans lived in New England? Or by visiting Boston can you see the future of Wyoming?"[72]

However, no undue importance should be given to these differences of opinion from Cowlesian ecology expressed by Gleason in 1909. They adumbrate future dissensions and illustrate the breadth of Gleason's early research commitments. But after the first flush of enthusiasm for physiographic ecology, few ecologists would not have acknowledged the importance of climatic change and plant migration to a full understanding of vegetational change. In 1911, Cowles stressed the importance of precisely those factors.[73] There was, as far as I am aware, no lasting dispute between Cowles and Adams, nor any lasting tension between their respective programmes of vegetation research. Indeed, in 1900, they had collaborated on a study of the relation between base-levelling and specific differentiation.[74] Cowles was later to endorse Gleason's further development of Adams's phytogeographic exemplar.[75] Gleason's criticisms were presumably directed principally against Clements - although this was not made explicit.

However, the criticisms expressed in the 1909 report were distinctively Gleasonian. They sprang from his having commitments to more than one programme of research. As I have said, they adumbrate future dissensions. But they should not be allowed to obscure the many features which his work had in common with Cowles's at this time. As we shall shortly see from our discussion of Gleason's sand-dune papers, it is clear that in the 1900s and 1910s, both men were working on similar problems in similar ways. More united them than divided them. They were participating in the creation of a common tradition.

On the Faculty of the University of Illinois

Shortly after his return from Isle Royale, Gleason left for New York to register for the degree of Ph.D. at Columbia University. His doctoral research was mostly done in the herbarium of the New York Botanical Garden and was entirely taxonomic. One of his supervisors was Nathaniel Lord Britton, the Director of the Garden, who set Gleason to work on the Vernonieae of North America.[76] But Gleason's ecological interest was not entirely in abeyance. During his time in New York, he put together his Isle Royale paper and wrote up the first of his studies of the inland sand-dunes of Illinois.[77] He was only a year in New York before he returned, with his doctorate, to join the faculty of the University of Illinois as an Instructor in Botany. In his 1944 autobiography, Gleason described his intentions upon leaving Columbia:-

> "Theoretically I had finished my education. Practically I had not completed it. I intended to specialize in ecology and I wanted to see and study all the principal types of vegetation of the world before I settled down permanently."[78]

Gleason was now only twenty-four and he was to go some way toward fulfilling both of these ambitions in the next few years. At Illinois he taught courses in morphology and taxonomy as well as ecology, but he was recognised as the ecology specialist on the staff:-

> "Ecology was to be my specialty at Illinois. It was a new subject everywhere and I was in on the ground floor."[79]

He ran a "beginning class" in ecology, with four field trips, for up to eighty students.[80] He also put on an advanced seminar course in ecology for a few especially interested students. His summers were spent in ecological research or teaching ecology at summer school. Of course, it must be remembered that, at this time, the University of Illinois was not well suited for taxonomic research having only a small herbarium and library. Ecological research had the advantage of needing less in the way of institutional facilities, and was thus more readily undertaken in the Mid-West, especially after the expansion of the inter-urban railway-system allowed easier access to a wide variety of field sites. But Gleason continued to concentrate on ecological research after he moved to the somewhat better-equipped University of Michigan in 1910.

The extent of Gleason's concentration on ecological research during the decade which followed his leaving New York can be gauged by the fact that between 1907 and 1918, he published fourteen papers which may be unequivocally classified as belonging to ecology or ecological plant geography, and only four on topics within floristics and taxonomy.[81] During this period in his career, he was, one might say, primarily an ecologist, with an important auxiliary interest in floristic botany.[82]

The first of these ecological papers to be published was entitled "The Botanical Survey of the Illinois River Valley Sand Region". It formed part of a series of three papers on the Sand Region published in the <u>Bulletin of the Illinois State Laboratory</u>.[83] It was preceded by an article by Hart on the area's geology and topography and followed by another article by Hart on the fauna. All three papers were the product of Hart and Gleason's joint study trips to the area - Gleason's field-work having been done in 1903 and 1904. The Sand Region of Illinois provided a most appropriate and appealing study subject for, as Gleason wrote:-

"The ecological study of sand-dune vegetation has in recent years attracted the attention of numerous American botanists, and many noteworthy contributions to it have been made. Dune vegetation is especially well adapted to ecological investigation, since the changes in the physical factors of the environment are usually considerable, the component associations are sharply distinguished, physiographic processes go on with comparatively great rapidity and the plant inhabitants show characteristic features in habit and structure. The vegetation of the dunes bordering Lake Michigan has been studied in detail by Cowles, while Rydberg, and Pound and Clements have described the sand-hills of Nebraska."[84]

Gleason's chosen study area was geographically intermediate between those of his famous predecessors. It was within the same floristic and climatic region. Gleason could thus readily address himself to unravelling the same vegetational processes as Cowles and Clements had studied. And the study area was so situated that it permitted not only the study of sand-dune vegetation but also, like those of Cowles and Clements, the interactions between the prairie vegetation and the forest. Furthermore, Gleason was able to shed some light on the phytogeographic origin of the prairie flora. By and large, the 1907 paper was a perfectly orthodox and thoroughly competent Cowlesian interpretation of successional changes in the dune vegetation due to biotic factors and the movement of the dunes by the wind. Being the first paper of his to be published, it is evidence of his successful recruitment to the new and growing specialty of plant ecology.

However, Gleason's first sand dune paper did exhibit at least one novel feature. Species composition was quantified. The species occurring in each study quadrat were grouped into classes, according to the number of individuals, "a signifying 1 to 5; b, 5-10; c, 10-25; d, 25-50; e, 50-100; f, 100-200; g, over 200; and o, none".[85] The numbers were "estimated for the most part although care was taken to make actual counts at intervals to avoid as far as possible any serious errors of observation".[86] Gleason made use of other methods of describing species abundance in his later work.[87]

Clearly this technique was a most rudimentary form of quantification. Yet its development by Gleason in 1907 is of considerable historical significance. Very little quantitative work, comparable in sophistication with even this simple numerical classification, had been done by North American plant ecologists prior to this date. Mention might be made of earlier work done by Clements in collaboration with Roscoe Pound in the context of their invention of the meter quadrat technique.[88] But the counting of species and individuals within quadrats was about the limit of Clements's development of quantitative techniques. For all his continual advocacy of physiology, quantification and more modern methods generally, Clements's work on plant communities was to remain primarily descriptive - as was the work of most of his contemporaries.[89] Gleason's 1907 paper, however, marked the beginning of his development of an increasingly sophisticated quantitative approach to vegetation - which was to make Gleason one of the pioneers of vegetational statistics.

As just noted, there was little interest in quantification among plant ecologists in the first decades of the twentieth century. But there was some other quantitative ecological work being done at Illinois at this time. Kofoid was applying quantitative techniques to the study of the composition and distribution of the freshwater plankton of the Illinois river.[90] Kofoid's work was pioneering both in the context of ecology in North America and as far as the worldwide study of plankton was concerned.[91] The first-ever quantitative study of plankton was only ten years old and the techniques involved had occasioned much controversy.[92] They were still novel. Gleason followed Kofoid's work closely.[93] Furthermore, also at Illinois, S.A. Forbes and his students were engaged in quantitative studies of the distribution of fish, insects and birds.[94] Gleason must certainly have been aware of Forbes's quantitative work - some of which was published in the same volume of the Bulletin of the Illinois State Laboratory as the Gleason-Hart papers on the biology of the sand areas. Thus, not only was the University of Illinois one of the few institutions in which ecological research and research into communities of organisms were being undertaken, it was also the location of some of the earliest quantitative ecology done in America. Doubtless, the examples offered by Kofoid and Forbes encouraged Gleason to apply his own numerical skills to the study of plant communities.

Differences and similarities with Clements

Between 1908 and 1913, Gleason published a series of papers on the vegetational problems of the Illinois area of the Middle West.[95] The most important paper of these Illinois years was the truly massive "The Vegetation of the Inland Sand Deposits of Illinois".[96] This paper, published in 1910, was one hundred and fifty-two pages long, not counting the photographs. It was the product of one of the most intensive field studies done by any American ecologist in the first two decades of the twentieth century (Gleason was supported in his field-work by a grant from the Botanical Society of America and a personal donation of $100 from S.A. Forbes).[97] Cowles's early studies on the shores of Lake Michigan or Cooper's famous studies following Cowles were not as large or as comprehensive in scope and vegetational detail as this 1910 paper of Gleason's.[98] And, although much the largest of Gleason's early papers, this was, as we have seen, by no means the only publication of his years in Illinois. At this time he must therefore have been one of the most prolific ecologists in America after Clements. Given the evident tendency for there to be a somewhat direct relationship between quantity of publications and achieved status in academic life, it is not hard to see these Illinois papers of Gleason's as announcing his challenge for a prominent role in the ecological profession. They certainly established that he was not subordinate to either Cowles or Clements in capacity for field research or ability to interpret vegetation. Proof of this is afforded by the fact that when in 1912, Norman Taylor named eight Americans "engaged in ecological work", Gleason was included together with Transeau, Shreve, Clements, Harper, Spalding, Harshberger and Cowles.[99]

Gleason's 1910 paper was not principally concerned with theoretical matters. But in it he expressed dissent from Clements on two important points. The first of these again illustrates Gleason's essentially floristic perspective on vegetation. Most ecologists routinely investigated the species composition of their chosen study areas. But it is the relative importance ascribed to this information by Gleason to which I wish to draw attention. The study of species presence and the relative numbers of individuals of each species was the primary means whereby Gleason sought to investigate and understand vegetation.

As we have seen in earlier chapters, this was not the only possible approach. Ecologists had used a variety of criteria to classify vegetation. They had considered habitat factors such as soil type or soil water content, or non-floristic vegetation features such as physiognomy or the spatial organisation of the plant cover.[100] Most relevant to our present discussion are the criteria used by Clements. The principal units of Clements's classification of vegetation, the formations, were identified by physiognomy - although in theory they were characterisable according to unified development. As we have seen in the previous chapter, Clements maintained that, by definition, all the dominants of a single climax formation must be of the same physiognomic type, since each distinctive physiognomic type represented a unified response by the vegetation to the regional climate.[101] Thus coniferous and deciduous trees could not both be climax dominants in the same formation. Where they occur together one or the other must be pre- or post-climax, that is part of a successional stage or a relict of a previous climax.[102]

Below the level of the major climatic units,the formations in Clements's hierarchical classification scheme, were the associations.[103] They were held to be units determined by habitat differences within the overall regional climate. Each association was said to belong to a definite habitat - river bank, sand bar, or mountain scree, for example. In practice, however, Clements used a combination of floristic and habitat criteria to determine the associations. This is reflected in his use of a nomenclature which made reference to both habitat and floristic features.[104]

In contrast to Clements, Gleason held that the non-floristic characteristics of a study area should be regarded as being secondary in importance, at least from the ecologist's point of view. Vegetation was constituted by the individual plants and it was as an object made up in this way that it ought to be studied:-

> " ... the differentiation of both minor and major ecological groups depends principally upon the plants themselves, the associations being distinguished by the specific composition, the formation by the general appearance, and the [floristic] province by the distribution of the vegetation. This is an extension of the idea already expressed, that the most important feature of the association is not the habitat but the plant."[105]

Discussing the classification contained in Clements's 1905 book Research Methods in Ecology, Gleason argued that "a classification of habitat rather than vegetation ... may lead to the uniting of radically different types of vegetation".[106] By "radically different types of vegetation" Gleason meant stands with significant differences in species composition. Contrariwise, Gleason also held that Clements arbitrarily separated associations which were in reality closely related because of similarities in species composition:-

> "The classification of associations by Clements is largely of this nature [i.e. a habitat classification] and in some cases leads to a wide separation of closely related associations or even to the placing of a particular area in two different groups. Thus a hydrophytic sand bar (cheradium) may be converted into a new xerophytic "formation" (syntidium) merely by the fall of the water in the river."[107]

Clements's argument that the classification of vegetation must ultimately rest upon climate and habitat factors was based on his axiom that the form of both the individual plant and the plant community were direct and proportional responses to the stimulus provided by the environment.[108] Again, Gleason argued differently:-

> "The plant itself is in many cases the controlling agent in the environment; the differentiation of definite associations is mainly due to the interrelation of the component plants; and the physical environment is as often the result as the cause of vegetation ... The establishment of a plant in the place which it occupies is conditioned quite as much by the influence of other plants as by that of the physical environment."[109]

The second point at which "The Vegetation of the Inland Sand Deposits of Illinois" departed from the theoretical framework being promulgated by Clements, was the question of the direction of succession. In the paper Gleason described "the first example of a reversed succession ... Clements said such a thing was impossible in nature".[110] To Clements, as we have seen, the formation was an organism.[111] Therefore all successional change must be developmental and progressive. Retrogressive change was as impossible for plant communities as it would be for an individual organism. Adults cannot spontaneously revert to being children. Therefore the reaction of the plants upon the environment must always usher in a higher, more mesophytic form of vegetation than the one which initiated the reaction. Only destruction of the vegetation by such factors as erosion, fire or overgrazing could produce changes in the vegetation which went against the developmental trend. Any vegetational change produced by the plants themselves must be in the direction of the climatic climax vegetation type. Thus Clements excluded, virtually by definition, all possibility that succession could be anything other than progressive.[112]

Gleason, however, interpreted the formation of ponds in the blow-out hollows of large sand-dunes as illustrations of true retrogressive succession. The process he discerned was as follows. The sand in the bottom of the hollow was stabilised by the moss Polytrichum which formed a dense carpet and produced a peaty layer of humus over the sand. This eventually became so thick that it gave a water-tight bottom to the hollow and prevented the run-off of standing water. A pond thus developed and was colonized by a typical association of pond plants. Now clearly this process was only temporary, but nevertheless it seemed to Gleason to be an instance in which vegetation reaction initially produced a more mesophytic vegetation from a xerophytic starting point and then reversed the trend toward mesophytism by producing a pond, that is a hydrophytic plant community.[113]

However it was not until 1917, seven years later, that Gleason explicitly made this example of reversed succession out to be a contradiction of Clements's developmental principle.[114] The discovery of this temporary reversal of the trend toward the mesophytic did not prevent Gleason from agreeing with the view of Cowles (endorsed by Clements) that all the "vegetation of a region is tending toward an ultimate common destiny".[115] Indeed, despite the above differences there was still, in 1910, much in common between the approaches of Clements and Gleason.

The common features between Clements's and Gleason's work in the 1900s and 1910s are evidence of Clements's enormous influence upon early American ecology. Such was the comprehensiveness and intellectual scope displayed in Clements's work that it had, in many respects, no rival. In the words of W.S. Cooper:-

> " ... Clements was the first to organize the field of dynamic ecology as a unified science covering the entire history of the plant population of the earth."[116]

Clements had investigated new research areas, developed new techniques, and proposed an organised format for ecology's embryonic methodology.[117] Contentious as much of Clements's theorising was, no-one else provided as detailed a general programme for the young discipline to grow into. His work could not be ignored and it was regularly drawn upon - even by those who disagreed with him vehemently and fundamentally.

There is certainly much in Gleason's 1910 paper - in his methodology, as exampled by his use of quadrats in transect across areas of transition; in his classification, as exampled by his use of an hierarchical system of syntaxa; in his nomenclature, as exampled by his use of terms such as 'consocies' and 'associes' - which displays his direct or indirect borrowings from Clements.[118] Clements and Gleason were later to differ on even more fundamental matters than those described above. Certain terminological Clementsianisms,which he used in 1910, were later to fall out of Gleason's usage. But mirroring the situation I have described for Cowles and Gleason, Clements and Gleason differed, at this time, within a shared tradition whose development and maturation they were both contributing to.

In 1910, Gleason moved to the University of Michigan. But this account of his work at Urbana would not be complete without mention of the fact that at the University of Illinois, Gleason was involved in the training of two young plant ecologists who were later to become prominent members of the profession. One of these men was Frank C. Gates, who eventually became Professor of Botany at Kansas State University and who was President of the Ecological Society in 1952.[119] Gates began his graduate work at Illinois under Gleason's supervision.[120] He also assisted with Gleason's field work in the Sand Region. When Gleason went to the University of Michigan, Gates followed him and completed his doctorate there. The other young ecologist was Arthur G. Vestal who, while an undergraduate at Illinois, likewise helped Gleason with his field work.[121] Vestal went on to take a doctorate under Cowles at Chicago, eventually returning to Illinois as Professor of Plant Ecology. He was Secretary/Treasurer of the Ecological Society in 1934.[122]

Physiological plant ecology

Some of the work Gleason did in collaboration with Gates is interesting in that it sheds further light on Gleason's perspective on vegetation. In 1914, Gates and Gleason published the results of a study of the rates of evaporation from different types of vegetation.[123] Evaporation was measured using the porous-cup atmometer. This is the only occasion I have come across on which Gleason used an instrument to make direct measurements of the physical environment.

The porous-cup atmometer had been developed by Barton Livingston of Johns Hopkins University.[124] Its use was in great vogue in the 1910s and 1920s. Atmometers had been employed in the field by Transeau, Fuller, Shreve, and several others, as well as by Livingston himself.[125] Accurate measurement of evaporation formed only part of a much larger research effort involving the comprehensive measurement of the physical habitat in an attempt to correlate environmental factors with the distribution of plants. Such a correlation was the principal aim of what was known as physiological ecology:-

> "The study of vegetation ... has brought its leading problems to the point at which they demand for their solution a precise knowledge of the functional activities of the plant and an equally precise knowledge of the environment."[126]

Physiological ecology constituted a major programme of research within the American plant ecology of the early decades of the twentieth century. It ran parallel with physiographic ecology and was of similar importance. As Cowles noted, in 1911:-

> "Plant ecology has a two-fold aspect: the one considers the individual organism and its component parts as related to environment; this, since it overlaps morphology and physiology may be called morphological and physiological ecology, or the ecology of plant structure and behavior. The other aspect considers plants en masse as related to soil and climate; this, since it overlaps physiography, may be called physiographic ecology, or the ecology of vegetation."[127]

Physiological ecology was, as its name implies, more directly associated with plant physiology proper than physiographic ecology was. Livingston, for instance, had studied plant physiology under

F.C. Newcombe at Michigan and had been laboratory assistant to both Newcombe and C.R. Barnes, who taught plant physiology at Chicago.[128] Livingston eventually became Director of the Johns Hopkins University Laboratory of Plant Physiology as well as holder of the Chair of Forest Ecology also at Johns Hopkins. To take another example, Daniel T. McDougal, the first Director of the Department of Plant Research at the Carnegie Desert Laboratory, had studied plant physiology at Purdue and been employed as a physiologist at the New York Botanical Garden.[129] In the hands of men such as these, ecology was indeed physiology extended into the field:-[130]

> "We have approached our problems in plant geography with the mental conception that they are merely problems in physiology, with all of the environmental conditions fluctuating and uncontrolled, but nevertheless measurable, and with all the activities of the plant in normal performance and also measurable, not by auxograph and balance, but by such features as distributional extent, habitat occurrence, communal behavior, relative abundance, size, seasonal behavior, etc."[131]

Investigations with the atmometer had led several ecologists to argue that changes in the rate of evaporation from plant communities ought to be considered as an important cause of plant succession.[132] Gleason and Gates argued from their atmometer data that change in the vegetation came before changes in evaporation rates and not as a consequence of these changes.[133] The moral that Gleason and Gates took from these atmometer experiments was entirely a negative one. They stressed the limitations of measuring instruments and the need for a prior understanding of vegetational dynamics on the part of the investigator if the use of instruments was not to mislead. In other words, Gleason's disagreement with Fuller and Transeau over the use of the atmometer took the same form as his disagreement with Clements over classification. In both instances, Gleason emphasised the primary importance of the study of the plants themselves over the study of the physical parameters. Gleason was no environmetrician. He resisted the allure of instrumentation and physiology. He adhered to the more conventional techniques of field botany - attempting to understand vegetation through the identification and observation of plants directly.

On the faculty of the University of Michigan

Gleason's teaching duties at Michigan were much the same as at Illinois - teaching ecology and taxonomy.[134] And in 1911 he had the additional task of teaching classes in ecology and general botany at the University's newly-established Biological Station on Douglas Lake in Northern Michigan.[135] In 1913, Gleason was made Director of the Station.[136] It was there that much of his later field work was done. It was, for example, in the environs of the Station that Gleason undertook the quadrat studies which supplied the data for his research into the statistical distribution of species within vegetation. This work was begun during the summer of 1912, when Arthur Vestal acted as Gleason's research assistant and "counted quadrats all summer".[137] Gleason continued to do field work at the Biological Station for several years after he had left the University of Michigan.

In 1913 Gleason took a year-long leave of absence from Michigan in order to fulfil one of his ambitions - to see more of the principal types of the world's vegetation.[138] With a research student, Bert Quick, as companion, Gleason went on a voyage around the world. The Asiatic tropics provided the especial interest of the trip. Gleason and Quick visited several sites in Ceylon, Borneo, Java and the Phillipines making floristic and vegetational observations. In the Phillipines, they stayed with Frank Gates who was then working for the College of Agriculture in Manila, and they benefited from his local knowledge of the vegetation types. On his return, Gleason published a series of short anecdotal and impressionistic descriptions of the types of vegetation and flora he had seen.[139] It is clear from these accounts that the tropical rain-forest made a lasting impression upon him:-

> "The marvelous richness and luxuriance of such a forest must be seen to be appreciated, and baffles adequate description. One scarcely enters the forest before he is impressed by the relatively great importance of the arborescent flora. The visitor finds himself giving all his attention to the trees, and neglecting almost completely the herbaceous plants along the side of the path. The number of species which comprise the forest is very large. More than four hundred have been reported for Mt. Makiling. Also they are widely scattered, so that a single small area contains a very large number. In a small arboretum of

> about seven acres, over two hundred species were found growing naturally. As a result, a group of trees of the same species is seldom found. The nearest neighboring individuals may be and usually are separated by a considerable distance, and the number of species is so large and confusing ... "[140]

His experience of tropical vegetation was, later in his career, to furnish him with evidence to support his revised conception of the nature of the plant community. On his return to Michigan, Gleason continued his research into the ecology and phytogeography of the region's woods and grasslands - investigating such matters as the role of fire in the maintenance of the prairie and the interactions between coniferous and deciduous woodland.[141] The vegetational history of the Middle West occupied him for many years, leading up to his publication in 1923 of a major paper on the subject.[142]

In 1916, Gleason attended the first summer field-trip meeting of the newly-formed Ecological Society of America.[143] This was held in San Diego, California. There he met Fred. E. Clements, apparently for the first time. The extent to which they disagreed was soon apparent:-

> "On our return trip [from a two-day trip into the mountains] I had the good fortune to ride in the same car with Clements, the noted ecologist ... Almost at once Clements and I got into an argument. It lasted until lunch, and after lunch until our car drew up in front of the ... hotel, where I was staying. As a parting shot when I left, Clements shook his long finger in front of my nose and said 'Now Gleason. My book on succession will be out next month, and it will be a test of your meristematic condition whether or not you can accept my ideas.'"[144]

The individualistic concept

But the publication of Clements's book Plant Succession did not silence Gleason.[145] As might have been predicted it had quite the opposite effect. Gleason was moved to write a critical riposte in which he expressed disagreement with Clements more explicitly than ever before:-

> "Ecological literature has recently been enriched by the publication of an exceedingly important book ... on the structure and development of vegetation ... For all

its contents the working ecologist is grateful, although it is probable that some of the more radical ideas of the author may be accepted reluctantly, and that others may be rejected altogether."[146]

Gleason took especial exception to four features of Clements's treatment of vegetation - his view that the unit of vegetation was an organism, his expansion of the scope of the vegetational unit to include not only the climax vegetation but all the successional stages leading up to the climax, his "introduction of several new terms into an already burdened terminology", and his exclusion by definition of possible exceptions to his deductive system.[147]

But as well as countering Clements on these specific points, Gleason set out an alternative set of propositions as to the nature of vegetation. It is worth noting that these embodied a theoretical position different not only from Clements, but also from that earlier adopted by Gleason himself. For instance, in 1910, Gleason, in his account of the sand-dune vegetation of Illinois, had explicitly accepted the generally-held opinion that plant associations were natural units of vegetation:-

"It is true that the distinctness of the associations is lost and their character greatly modified by the effects of civilisation but experience in natural conditions justifies the statement that associations are definite organized units and that all vegetation is composed of them, either mature and fully differentiated or in process of organization. It is as difficult to formulate a satisfactory definition of an association as of a species, and as unnecessary. For the present it may be considered that it is a homogeneous area of vegetation in which the interrelations of the component individual plants permit them to endure the physical environment."[148]

This differentiation of the vegetation into definite associations was brought about by the plants themselves "through their modification and control of the physical features of the environment."[149]

Also, Gleason had earlier been prepared to think of the plant association as analogous to the taxonomic species:-

"The areal distribution of an association may be compared to the distribution of a species. Both are irregular in outline, although co-extensive with certain combinations of environmental factors. Both consist of scattered members independent of each other, but related by a common genesis and common demand upon the environment. Both show minor local and broad geographical varieties. The former are illustrated in the association by the consocies; the latter, in the species by the subspecies ... "[150]

But by 1917, Gleason was no longer happy with this analogy:-

"While the similarity of vegetation in two detached areas may be striking, it is only an expression of similar environmental conditions and similar surrounding plant populations. If they are for convenience described under the same name, this treatment is in no wise comparable to the inclusion of several plant individuals in one species."[151]

Gleason's dissatisfaction with the taxonomic analogy followed from the fact that he was no longer prepared to accept that vegetation universally existed in natural units. Gleason did not deny that there were units of vegetation which might be recognised in the field, nor did he deny that it was useful to classify vegetation into units, but:-

" ... the great mass of ecological facts revealed by observation and experiment may be classified in different ways."[152]

No one classification of vegetation was uniquely natural.

Gleason noted that many of the techniques used in the study of vegetation depended on the assumption of vegetational uniformity for their utility since "a small area can be chosen for intensive study which exhibits faithfully the average structure of the whole association".[153] He acknowledged, as he had done in 1910, that the dominant species of any given association exercised a certain influence over the environmental conditions experienced by the subordinate species. Therefore subordinate species tended to be somewhat similar throughout the area of a given set of dominants. But visually striking as this apparent uniformity within an association might be, and useful as its assumption was heuristically, it was not absolute. The environmental control of the dominants was not by itself enough to enforce uniform species composition over wide areas of an association. The physical environment varied continuously and, Gleason argued, "no two species have identical environmental demands".[154] Therefore, despite the fact that a particular set of subordinate species was often to be found occurring underneath a given dominant species or a given dominant vegetative form, plants did not occur in precisely repeating groups. Individuals of the same species were capable of growing in different habitats, and had different associated species in different localities:-

> "With one environmental factor near the optimum, others may apparently be near the minimum: thus the tamarack, which in southern Michigan is confined to peat bogs, in Isle Royale occurs even in crevices in vertical rock cliffs."[155]

When one allowed for further obstacles in the way of the establishment of uniform species composition - such as the vicissitudes of migration and invasion - it was clear that there were too many variables involved in determining which plant species grew where for vegetation to remain constant over a large area or to repeat itself exactly in two localities. Plant species had individual requirements and properties and distributed themselves accordingly.[156] Migration served Gleason as a good example of this dependence. Each species moved at its own rate - depending on such matters as the mobility of its seeds or spores, species-specific response to physical factors, accidents of dispersal, variation in seed production, and the proximity of parent plants. Clearly the composition of any given piece of vegetation was dependent on whether all the species capable of living in that locality had succeeded in migrating to it. Thus associational composition was dependent on the individualistic behaviour of the plant species.

Gleason argued that when one examined vegetation in the field, one indeed found that no two areas had identical composition as measured by component species and the relative numbers of individuals of each species. He had studied the beech-maple forest around Douglas Lake and found constant variation between sites and "much greater differences are found when these are compared with the beech-maple forest of Southern Michigan, 500 km away."[157] Variation was continuous even within a vegetation type as apparently definite and homogeneous as beech-maple, but "still the beech-maple forest has always been interpreted as a single association of wide extent."[158]

Gleason still considered it legitimate to call vegetational features such as the beech-maple forest 'associations'. The designation was useful and common practice among ecologists:-

> "In the same limited region, that is with the same surrounding population, areas of similar environment, whether continuous or detached, are therefore occupied by similar assemblages of species. Such an assemblage is called a plant association."[159]

There were indeed often naturally occurring sharp discontinuities between one sort of vegetation, one association, and the next. But such discontinuities were not sufficiently numerous or sufficiently consistent to allow the construction of a comprehensive classification of vegetation into natural units:-

> "The physical factors of the environment generally vary gradually in space ... Such gradual and progressive variation of environment would normally lead to equally gradual and progressive changes in vegetation ... "[160]

Under these conditions Gleason argued, where one association finished and another began was a matter of judgement:-

> "Whether any two areas, either contiguous or separated, represent the same plant association, detached examples of the same one, consocies, or different associations, and how much variation of structure may be allowed within an association without affecting its identity, are both purely academic questions ... "[161]

Gleason had come to believe that all the collective phenomena of vegetation depended on the individualistic behaviour of the component plants. Therefore the recognition of vegetational units could not always be based upon the existence of natural divisions within the vegetation itself:-

> " ... since the association represents merely the coincidence of certain plant individuals ... "[162]

This individualistic perspective led Gleason to make a strong criticism of the homology Clements had made between the plant community and the individual organism.[163] Gleason pointed out that the later stages of a plant community's development did not spring endogenously from within its immature stages. Rather they were the result of the invasion of new member species from outside the community. As we have already seen, to Gleason migration was an individualistic phenomenon - each species moved at its own rate. Whole associations did not migrate together.

Furthermore, vegetational change need not in Gleason's opinion be developmental. It could be retrogressive, trending away from the mesophytic - a pond could become established upon a sand-dune as Gleason had described in 1910. Vegetational change toward mesophytism could be entirely absent:-

> "Theoretically, all associations of a region tend to culminate in the establishment of a climax. Many associations, however, occupy their ground so tenaciously that there is little or no observable evidence that they are ever replaced by the association ordinarily considered to be the climax of that region."[164]

Gleason was thus no longer a believer in the monoclimax hypothesis. Succession was individualistic, like all the other processes within vegetation, not propelled by necessary inherent vegetational or climatic principles.

For all the above reasons, in Gleason's view the origin of a new plant community, its successional development and its eventual disappearance were not at all comparable to the stages in the life-history of an individual plant:-

> " ... in sharp contrast with the view of Clements that the unit of vegetation is an organism which exhibits a series of functions distinct from those of the individual and within which the individual plants play a part as subsidiary to the whole as that of a single tracheid within a tree."[165]

On the contrary, "the phenomena of vegetation depend completely upon the phenomena of the individual".[166]

With the publication of "The structure and development of the plant association" in 1917, Gleason moved from being a more or less typical young physiographic ecologist to take up a distinctive position of theoretical heterodoxy. His 'individualistic concept' or 'individualistic hypothesis', as it was to become known, was to remain controversial, guaranteeing him a degree of notoriety among ecologists, for fifty years.[167]

The mainstream of ecological opinion

Had Gleason confined his criticisms to Clements's organicism, it is unlikely that he would have been perceived as unconscionably heterodox by the majority of his ecological peers. This is a crucially important point. Several authors have described the polar dichotomy between Clements's and Gleason's views on the nature of the plant association.[168] Certainly the views of these two ecologists were radically different. But it has been too often assumed that these two points of view represent the entire extent of the debate. Certain commentators, notably Tobey and Worster, have portrayed this controversy as being fought between a Clementsian majority, on the one hand, and a lonely Gleason, on the other.[169]

The possibility of a broad middle ground between the two extremes has seldom been remarked upon. But such a body of opinion did exist. Clements's work had certainly been influential. But many American ecologists, perhaps a majority, did not accept "the pure milk of the Clementsian word", any more than they accepted the individualistic hypothesis.[170] I have been unable to find the Clementsian organismic analogy within the independent work of J.E. Weaver whom Ronald Tobey names as Clements's chief apostle and collaborator.[171] Nor can it be found in the work of Bergman and Stallard who were students of Clements at Minnesota, whose research was done under Clements's direction, and whose field practice and interpretation of data were clearly and explicitly based upon the exemplar of <u>Plant Succession</u>.[172] If the organismic concept cannot be found in these authors, it seems unlikely that it was widely used within the specialty. The early volumes of <u>Ecology</u>, the journal of the American Ecological Society, first published in 1920, contain very few examples of its employment by plant ecologists. Overall the evidence seems to support Duff's contention that, in this respect, Clements "was out on a theoretical limb".[173]

The fact that the organismic analogy was seldom used in technical contexts supports the argument I developed in the previous chapter that its principal function was an ideological one - fashioned by Clements's need to exercise suasion within a lay constituency. An important secondary purpose seems to have been in pedagogy. There is, for example, an important exposition of the organismic analogy in W.B. McDougall's 1931 textbook.[174] It is also referred to frequently throughout Clements and Weaver's 1929 textbook.[175] (It is strangely absent from Clements's earlier 1907 textbook.)[176] However as far as the technical context of ecological research and theory-making is concerned, the organismic analogy was not generally employed.

An awareness of the existence of a large body of opinion which disagreed with both Clements and Gleason is essential to a proper understanding of this period in the history of American plant ecology. Any other interpretation oversimplifies the complexity of the debate and, indeed, greatly exaggerates Clements's intellectual dominance. He was important, but not that important. It also ignores the attitude of major plant ecologists, such as W.S. Cooper and G.E. Nichols, who were to be crucial foci of research and, especially in Cooper's case, graduate teaching throughout the twenties and thirties.

To get an impression of opinion somewhere near the centre of the spectrum between Clements and Gleason, let us look at several articles, produced by American ecologists in the second and third decades of the twentieth century - beginning with "The interpretation and application of certain terms and concepts in the ecological classification of plant communities" - published by George Nichols in the same year as Gleason's first presentation of his individualistic concept.[177] Nichols's reading of Cowles was reflected in his work.[178] He was clearly doing Cowlesian ecology:-

> "During the past seven years much of the writer's study has been along the line of local physiographic plant ecology ... "[179]

Nichols proposed a formal system of classification of vegetation - specially designed so as to be compatible with the practice of physiographic ecology:-

> "The groundwork for such a classification is afforded by the principle of succession, the fundamental bearing of which on the relationship and evolution of plant communities has been indisputably established by the work of Cowles, Whitford, Clements, Moss and others ... The scheme of classification itself is by no means wholly new or original. It is the outgrowth, and perhaps not a very radical modification of the classification originally devised by Cowles."[180]

Nichols's proposed classificatory scheme was quite complex and its details need not concern us here. However in describing the rationale behind his system, Nichols necessarily expressed his opinion on several points of the theory of vegetation.

Nichols's system differed from Clements's in several ways. One of the most important was that he did not acknowledge the physiognomic formation to be the fundamental unit of vegetation. To Nichols, the fundamental unit was the association. At least in theory, uniformity of habitat defined the association. It was:-

> " ... any group or community of plants, taken in its entirety, which occupies a common habitat ... an essentially uniform environment."[181]

Unlike Gleason, but like Cowles, Nichols made use of the taxonomic analogy:-

> "If the association is regarded as an ecological species and the edaphic formation constitutes an ecological genus ... "[182]

This reflected his conviction that the association was a natural unit of vegetation.

Floristic criteria occupied a secondary place, behind habitat criteria, in Nichols's classificatory system. Variation in species composition was acknowledged by the proposed sub-divisions of the fundamental unit - which Nichols termed 'consociations' (where the variation concerned the dominant species), or 'societies' (where the variation concerned species of secondary importance).

The association, as conceived of by Nichols, was not a complex developmental unit in the Clementsian sense of including all the successional stages leading up to the climatic climax. Nichols defined the association as consisting of a single "stage in a given successional series", not the entire series considered as a single entity.[183] Vegetational development was however accommodated within the classificatory scheme in that associations held to be successionally related to one another were grouped together into an 'association-complex'.[184]

But Nichols's association-complexes were not quite identical to the Clementsian formations. For Nichols, while accepting that there was an overall trend toward increased mesophytism within any given area of vegetation, did not believe that all the successional series in that area were necessarily destined to achieve a single common vegetation type. That is to say, like Gleason, he did not accept the monoclimax hypothesis, which was one of the most important elements of the Clementsian theory:-

> "Now it is commonly stated or implied in ecological literature that in every region, as the logical consummation of progressive successional changes, the vegetation of all soils and all types of topography is destined eventually to acquire the same degree of mesophytism that characterizes the regional climax association-type; that, while in unfavourable situations the influence of certain habitat factors may diminish the rapidity of the succession, it does not alter the final outcome; that ultimately ... the regional climax is destined to be attained in all areas ... This is the working hypothesis which the writer followed in his earlier field-studies; but observations continued over a number of years have made it seem increasingly evident that such an assumption is untenable from the standpoint of contemporaneous dynamic plant geography."[185]

Nichols argued that habitat factors, such as wind on an exposed sea coast, might place a permanent limit on the degree of mesophytism that vegetation within that habitat could attain. Mature vegetation-types in which succession had been altered in this way constituted "edaphic climax associations".[186] They and their successional stages could be naturally grouped together into "edaphic formations". Nichols was, thus, an adherent of the polyclimax theory - the view that it was possible to have more than one permanent type of vegetation occurring within an area of uniform climate.

The polyclimax view was shared by many American and European ecologists. Schimper, for instance, had been the first to propose a special nomenclature for edaphic climax vegetation-types.[187] Tansley, when reviewing Clements's Plant Succession, had expressed agreement with Schimper and pointed to the absence of any recognition of the existence of non-climatic permanent vegetation-types as one of the major defects of Clements's book.[188] But American opinion was divided on this matter. Cowles, for instance, had proposed a monoclimax hypothesis before Clements.[189] And in 1911 he had forthrightly re-expressed the theoretical basis for such a view:-

> "At the close of the vegetative cycle there is no such universal feature as the base level of the

physiographer, since the final vegetative aspect varies with the climate, and hence is called a climatic formation. In the eastern United States, the final stage is a mesophytic deciduous forest; farther to the north and in the Pacific states, it is a coniferous forest; in the great belt from Texas to Saskatchewan, the final stage is a prairie; and in the arid southwest, it is a desert. In every case, the ultimate or climatic plant formation is the most mesophytic which the climate is able to support in the region taken as a whole."[190]

Cowles's student, W.S. Cooper, in his comprehensive application of the Cowlesian system to the forests of Isle Royale, had argued, on the basis of field data, that all the successions he observed in the Lake Forest were leading toward a common goal, a single climax-type - the balsam-birch-white spruce forest.[191] It is not surprising that Cooper discerned a single climax on Isle Royale, for he had gone to Lake Superior with the specific intention of identifying the climatic climax of the Lake Forest:-

"Eastern North America North of Florida and Mexico is divided into two great phytogeographic regions, the eastern deciduous forest and the northeastern conifer forest. In each of these a number of lines of succession may be traced, all of these of a region leading to a certain forest type as the final or climax stage ... The purpose of the present work was to determine the climax forest of Isle Royale, its composition and character, and to trace the various lines of succession leading to it."[192]

But Cooper's willingness to accept, with reservations, the monoclimax hypothesis did not make him a Clementsian.[193] Neither Cowles nor Cooper nor Nichols ever employed Clements's organismic conception of the plant community. Cooper repeatedly expressed his dissent from it:-

" ... we note the thesis, declared to be fundamental, that the unit or climax community is an organic entity, with structure and functions corresponding to those of an individual organism. This assumption colors the whole of Clements' treatment, and in the opinion of the writer, detracts seriously from the usefulness of his contribution."[194]

and again:-

"Many ecologists have accepted Clements's thesis that 'the developmental study of vegetation necessarily rests upon the assumption that the unit or climax

> formation is an organic entity. As an organism the formation arises, grows, matures, and dies'. Thus set up as a foundation stone - as the corner stone, indeed, of the whole edifice - it demands consideration. Although by no means the first to voice opposition, I cannot refrain from expressing vigorous dissent from the categorical statement quoted above."[195]

He concluded, after a detailed discussion:-

> "The assumption that the vegetation-unit is an organism, used as a foundation stone of the edifice of dynamic ecology, is fallacious and should be abandoned."[196]

Cooper also expressed dissent with Clements over the a priori requirement that all the dominants of any given climax need necessarily be of a single life-form. Indeed he commended Gleason on his vigorous protest against Clements's "unwarrantable framing of rigid, subjective concepts".[197]

Thus we can conclude, from this brief review of opinion in the profession, that there was far from universal acceptance among American ecologists of the Clementsian doctrine, in its entirety. In particular there was much disagreement over the question as to whether the plant formation could be regarded as equivalent to a biological organism. Thus, if Gleason had confined his criticism of Clements to the question of organicism, or to Clements's "introduction of several new terms into an already burdened terminology", or his enlargement of "the scope of the vegetational unit [so] that it includes ... not only a climax but also all the vegetational series leading to the climax", or his rigid petitio principii definitions, it is probable that Gleason would not have irrevocably offended moderate opinion within the specialty.[198] If the above had been the limits of Gleason's critique, it is unlikely he would have seemed any more radical than the eminently respectable W.S. Cooper - with whose view of vegetation Gleason expressed much sympathy.[199]

What really differentiated Gleason from his contemporary ecologists was not his aversion to the plant association being regarded as an organism, but his criticism of the much more widely held view that the association was a definite entity of some other, less highly integrated, variety. Cooper expressed what I take to be the majority view:-

"It seems to me that plant communities exist, that they are definable and comparable and therefore constitute a legitimate field of study. Naturally they are not nearly so sharply defined as individual organisms."[200]

Against Gleason's contention that "the phenomena of vegetation depend completely upon the phenomena of the individual", Cooper argued that:-[201]

"Assemblages of plants or of animals are subject to special laws, so that their mass action is not equivalent to the sum of the action of the component individuals."[202]

On this matter Cooper regarded Clements's and Gleason's views as equally dissentient:-

"His [Gleason's] paper was a useful corrective to the tendencies toward the opposite extreme. I think the truth lies somewhere in between."[203]

That is to say, plant communities were integrated entities in their own right. They had distinctive properties. Their study required autonomous forms of explanation. But they did not possess such a high level of integration as to be equivalent to the individual biological organism.

Nichols's view of the level of integration within the plant community was also different from Clements's. He was however prepared to employ a broad analogy between plant communities and individual organisms:-

" ... a plant association may be regarded in its entirety as an organic entity, and as such it occupies a position in the field of ecological plant sociology which is homologous in a general way to that occupied by an individual plant or specimen in such fields of botany as plant morphology or plant taxonomy. As integral parts of the larger community, plant societies bear a relation to the association which is somewhat analogous to that borne by the various organs of an individual plant to the plant as a whole."[204]

But Nichols located the level at which the processes of organic integration were effective quite differently from Clements. What Clements regarded as an organic entity, Nichols terms an aggregate. For example, the pitch pine 'entity', according to Clements, included within it all the pitch pine communities in existence and also all successional stages developing or potentially developing into pitch pine communities. In Nichols's view, however, the organic entity was a concrete piece of vegetation, a single plant community - or individual stand or a close group of stands of pitch pine trees. This was the level at which integrative community processes were discernable:-

> "To me the aggregate view of the association seems altogether too intangible to be of practical value; at any rate I am extremely reluctant to regard the association in this sense as being in the nature of an organism."[205]

Nichols's view is therefore not identical to Cooper's, but, like Cooper, he stands somewhere between Clements and Gleason on the question of the organic (or otherwise) nature of the plant community. So, too, did George Fuller, another student of Cowles, who in a review of American opinion on the nature of the plant community, published in 1918, was the first to polarize the views of Clements and Gleason as representing the ends of the spectrum of American opinion.[206] Fuller agreed with Clements that the plant community was "an entity comparable to some extent at least to an organism" but he saw this only as a useful analogy.[207] He had reservations about the full-blown homology postulated by Clements.

We have now considered all the major articles, written by American ecologists in the late 1910s and early 1920s, that discuss the nature of the plant association. With the exception of Gleason's, they all represent the opinion that the plant community was more than the sum of its constituent individuals. The phenomena of vegetation were not simply the phenomena of individual plants. Integrative processes operated at the level of the vegetation itself, at least in certain circumstances:-

> "Viewed as a concrete piece of vegetation, any association may be regarded as an entity, or even as an organic entity; but the only associations which may at all reasonably be likened to organisms are those in which there is active commensalism; whose constituent plants, in varying degree, exhibit the phenomena of competition, priority, dependence and mutuality. These relationships are most highly developed in climax communities."[208]

Thus the plant community was generally regarded as a real natural unit. But it was a unit not quite as integrated, not quite as closely similar to a biological organism as Clements claimed. Its development was not strictly comparable to the life-cycle of an individual plant or animal. As Nichols put it:-

> "Most ecologists ... would concede ... that the likening of the association to an organism must necessarily be taken, very largely, as a figure of speech."[209]

The tripartite division of ecological opinion which I have outlined here - Clements, the mainstream, Gleason - has not been previously recognised by historians. However it was recognised by contemporary observers. As Gleason categorised it:-

> "Out of the thousands of pages of literature which have been used in expounding various views on the matter, three well marked theories may be chosen ...
>
> 1. The association is an organism, or a quasi-organism, ... made up of individual plants and animals held together by a close bond of interdependence ... with properties different from, but analogous to, the vital principles of an individual, including phenomena similar to birth, life, and death, as well as constant structural features comparable to the structures of the individual [the view of Clements]
>
> 2. The association is not an organism, but is a series of separate similar units, variable in size but repeated in numerous examples. As such, it is comparable to a species. Under this view, the association is ... capable of typification by one or more of those pieces which most nearly approach the average or ideal condition. [the view of what I have termed the Mainstream]
>
> 3. The vegetation unit is a temporary and fluctuating phenomenon, dependent, in its origin, its structure, and its disappearance, on the selective action of the environment and on the nature of the surrounding vegetation. [the view of Gleason]"[210]

Gleason, Clements, Cowles, Cooper, Nichols and Fuller were all practitioners of what they called 'dynamic' ecology - employing large-scale vegetational units, and being particularly concerned with vegetational change between and within these units. They worked with a common tradition. But within that tradition, Clements's and Gleason's views on the nature of the plant association were regarded by most observers as being equally extreme, albeit in opposite directions.

At the New York Botanical Garden - quantitative investigations

Professionally and personally, Gleason's years at Michigan were successful ones. He was being groomed to become head of department upon the retiral of the incumbent, F.C. Newcombe. He had married and built a house to his own specifications. But the pay was comparatively poor and salary increments were not so large or as regular as Gleason thought his due. He was also frustrated by having to teach a course in elementary botany to pharmacy students. Meanwhile he had been keeping up his contacts with the New York Botanical Garden. In 1912, Britton received new collections of Vernonia from Cuba and he invited Gleason to come to New York to study them. Gleason was again invited to New York in 1918. Before he returned to Ann Arbor, Britton offered him a permanent post at the Garden. The position was that of First Assistant - second in rank in the Garden and equivalent to Assistant Director:-

> "I was in a quandary. I knew that New York would be a dreadful place to live, especially in comparison with our Ann Arbor home. I knew that we would find it difficult to get acquainted with any people outside the Garden staff. I knew I would have shorter vacations and more rigidity in my working hours. But I also knew, on the other side of the ledger, that I would have a considerably larger salary and a far better chance for research. I knew that I was getting tired of teaching the same old subjects over and over."[211]

Gleason accepted Britton's offer and in February 1919, at the age of 37, moved to New York.

Inevitably, in such an institutional setting, the principal direction of Gleason's research effort shifted, from ecological toward taxonomic investigations:-

> "Britton wanted me to take up this vast problem [the Flora of northern South America] for my life work, and decided that a trip down there would be the best way to arouse my interest. Since I spoke no Spanish, the only place to send me was British Guiana."[212]

Thus began Gleason's investigation of tropical flora which was to occupy him for eighteen years until he eventually forsook it to devote himself to revising Britton and Brown's Illustrated Flora of North America.[213]

But he did not abandon ecology altogether, despite his work in taxonomy and heavy administrative duties. In 1923, he returned to the Michigan Biological Station to teach a summer course and to do ecological research. George Nichols was also at the Station during that year.[214] He and Gleason were close friends and Nichols had acknowledged how Gleason's "stimulating and suggestive advice" had helped him in preparation of one of his papers.[215] They were to remain on good terms until Nichols died in 1939.[216] But now something was different:-

> "Nichols and I were the best of friends, but he simply would not discuss ecology with me. I knew why; it was because his ideas and mine were so radically different."[217]

Gleason was again at the Station in 1931, continuing the quantitative studies begun in 1912. He returned also in 1933 and 1935. Membership of the staff of the New York Botanical Garden did not mean that Gleason immediately ceased to produce ecological articles. His important technical and quantitative paper "Some applications of the quadrat method" was published in 1920.[218]

In the following pages, I shall consider Gleason's quantitative work in some detail. I do this because such study sheds important light on the precise nature of his conception of vegetation. We must understand the exact character of his individualistic hypothesis if we are to understand how it was modified by the ecologists who revived it after the Second World War. Such modification will be discussed in the following chapter. Secondly, the reception the quantitative aspect of Gleason's work received says much about the general attitude of ecologists toward quantitative investigations in the nineteen-twenties and -thirties. As we shall see in the next chapter, the revival of the individualistic hypothesis coincided with the rise of interest in quantitative methods. That the individualistic hypothesis was quantitatively testable was one of its important attractions. Thirdly, close scrutiny of Gleason's vegetational statistics shows that even mathematical expressions of the nature of vegetation are structured by prior interests. Gleason's vegetational statistics express his commitment to the floristic level of investigation. They are amenable to the same explanation as the other expressions of that commitment. The apparent objectivity of quantitative techniques does not mean that mathematical forms of knowledge about vegetation are uniquely determined by input from the natural world.

Gleason had employed the quadrat technique regularly since 1903. In his study of the development of two plant associations in northern Michigan, he had used data from quadrats fixed out over three seasons between 1915 and 1917. Like Clements, he believed that the quadrat method facilitated an objective understanding of vegetation structure and changes:-

> " ... in all cases of verbal description, the result unconsciously and unavoidably embodies the author's idea of the conditions, rather than the actual and impersonal facts, in that conspicuous species may be emphasized although possibly relatively unimportant, while important but comparatively inconspicuous species may be neglected. While the quadrat method is by no means a panacea for all these difficulties, its proper combination with verbal description and photography does much to aid the observer in securing a thorough knowledge of the association and in more satisfactorily expressing its structure in terms intelligible to his readers."[219]

But Gleason's view of the nature of the plant association had certain consequences for the application of the quadrat method. Outlining these was the first purpose of the 1920 paper:-

> "The use of a chosen quadrat in representing the structure depends absolutely on the theory of the homogeneity of the association ... If the association were absolutely homogeneous ... any quadrat could be chosen to represent the vegetation."[220]

But since no association was perfectly or essentially homogeneous, the location of quadrats became a crucial matter. The investigator could not simply place them where he happened to regard the vegetation as typical since the data thus produced would not necessarily constitute an objective representation of the association as a whole:-

> " ... the quadrat method itself, as ordinarily used, offers no aid in the selection of this typical area, so the actual choice invariably represents the observer's idea rather than the impersonal facts."[221]

Gleason therefore argued that large numbers of quadrats had to be set out in order to describe adequately a single association. He recommended the use of one hundred since this number made computation easier. Also he advocated that these plots be "chosen at random to avoid the personal element".[222] Gleason did not, however, mean 'random' in the modern strict sense.[223] He simply placed the first plot 'anywhere' and located the others in some pre-determined relation to the first. For example, they might be in a straight line or around the corners of a square. Statistically inadequate as this may seem by present standards, it was quite different in principle to the then accepted practice whereby the investigator placed the plots where he had, by inspection, decided the vegetation was most typical. The resulting data were then used to describe the structure of the association.[224]

The second purpose of the 1920 paper was to display Gleason's ideas as to how the structure of vegetation could be statistically expressed. The primary advantage Gleason saw in the quadrat method was that it yielded neat quantitative data. The quadrat "does constitute the only practicable means for the quantitative study of the association".[225] Quadrats, therefore, were the basis of Gleason's statistical study of vegetation.

The principal quantitative measure of vegetation which Gleason extracted from the quadrat data was the frequency index [F.I.]. The use of this measure had been pioneered by the Montpelier botanist P. Jaccard in 1901.[226] The frequency index is the ratio of the number of quadrats in which a particular species occurs to the total number of quadrats used. [Clearly the value of the frequency index of each species is dependent on the area of the quadrats used. In forest, Gleason generally used one metre quadrats]. Thus, a quantitative description of a given piece of vegetation might take the form of a list of species ranked according to their frequency indices. Any species with an F.I. of 0.60 or more was deemed to be important.

The frequency indices could be used to construct 'major quadrats'.[227] These were larger than the original quadrats - their size being so determined that any one contained all the major species of the association as well as a number of other less important ones.

More precisely, the size of the major quadrat was arrived at by determining at which size all the important species (original F.I. greater than or equal to 0.60) would have their F.I.s increased to 0.99 or more. Once determined, a major quadrat could be cautiously regarded as 'a fair sample' of the association in its entirety, and could be used as the basis for further intensive study or for teaching purposes.[228]

Using probability considerations, Gleason derived an equation for F.I. If n plants are distributed at random over q quadrats, the probability of any one quadrat being occupied is $1 - (1 - \frac{1}{q})^n$. Which is to say:-

$$\text{F.I.} = 1 - (1 - \frac{1}{q})^n \qquad (1)$$

This became known as Gleason's Formula.

If the F.I. for any species had been calculated from the field data, Gleason's Formula allowed n - the expected total number of individual plants of that species within the quadrats - to be derived.

$$n = \frac{\log\,(1 - \text{F.I.})}{\log\,.99}\,, \qquad \text{where } q = 100 \qquad (2)$$

The actual number of plants was nearly always greater than the value of n calculated in this way, due to the fact that few plants are randomly distributed.

Gleason's Formula could also be used to determine the required size of the major quadrat. If F.I. is given the value 0.99 (the desired F.I. for all important species in a major quadrat) and the total number of plants of a species with original F.I. 0.60 (calculated using equation 2 above) is taken as the value of n, then Gleason's Formula could be solved for q. This gave the number of larger quadrats into which the original 100 quadrats must be redivided so that all the species with original F.I. 0.60 or more would show F.I.s of 0.99 or more. Thus, if q was 20, the original 100 quadrats were redivided into 20 larger quadrats. Thus the major quadrat would be five times as large as the original. Despite the discrepancy between the actual and the expected values of n, Gleason concluded that:-

> " ... experience has shown that it [the method of calculating the size of the major quadrats] gives surprizingly good results. On the average four major quadrats out of five, the location of which is chosen at random, present all the important species for which they were computed."[229]

Gleason concluded the paper by indicating how the frequency indices could be used to improve Jaccard's community coefficient (C.C.) which was designed to express numerically the degree of similarity between two areas of vegetation. Jaccard had simply divided the number of species to both areas by the total number of species observed in the two areas. Every species was thus of equal significance. The technique failed to allow for the greater importance with plant communities of a few very abundant species. However, Gleason weighted each species with its frequency index. Thus his community coefficient was the sum of the frequency indices of species common to both areas, divided by the sum of the frequency indices of all the species found over the two areas. This produced C.C. values which coincided more closely to visual impressions of similarity.[230]

Gleason's 1920 paper was very much a pioneer effort. His statistical ecology was distinctive and innovative. These qualities were further exhibited in two other quantitative papers Gleason produced in the 1920s.[231] These were both on the relation between area and the number of species. Obviously larger areas of vegetation generally contain more species than the smaller areas. In 1921, the Swedish botanist Arrhenius had attempted to express mathematically the relation between the size of the area and the number of species.[232] He suggested the formula

$$\frac{\text{Area 1}}{\text{Area 2}} = \left[\frac{\text{no. of species in Area 1}}{\text{no. of species in Area 2}}\right]^n$$

where area 1 and area 2 are portions of the same association, and n is a constant for each association. In 1923, Gleason published calculations which showed that Arrhenius's equation gave erroneous predictions under several circumstances, and especially when applied to areas of a square kilometre or more - in which cases the solutions gave either absurdly high or absurdly low predictions, depending on the value of the exponent, n.[233]

Gleason pointed out that, if an association was perfectly uniform, then a single quadrat of suitable size would be sufficient to encompass its entire complement of species and larger areas would produce no increase in the number of species found. However, in fact, not all species were uniformly distributed. Many were localised and absent from certain parts of the association. Thus counting more quadrats did in fact increase the number of species found. But only up to a point - associations were overall quite uniform in composition. Indeed it was on the basis of such uniformity that pieces of vegetation were identified as associations. Thus as more quadrats were counted, the rate of increase in the number of species found should show a steady decline. Arrhenius had erred, according to Gleason, in using too small a size of quadrat - only a single square decimetre. Even counting a total of three hundred such quadrats would not be sufficient to show the eventual reduction in the rate of increase of species.

As an alternative to Arrhenius's exponential formula, Gleason proposed a logarithmic relationship between species and area. However he was, in 1922, unable to say precisely what this relationship might be. He stated he was handicapped in his study of the matter by the fact that a large amount of quantitative data collected for statistical research had been lost. Presumably this had occurred in the fire which, in 1913, destroyed the south wing of University Hall in Ann Arbor in which the Botany Department of the University of Michigan was then situated.[234] (Some of these lost data were presumably those collected by Vestal in 1912 - for Gleason never published the results of those early quantitative investigations.) However, in 1923, Gleason undertook further quantitative fieldwork, again at the Biological Station on Douglas Lake, with the help of several undergraduate assistants.[235] The results of this investigation were published in 1925.

Gleason was now able to propose the formula

$$\frac{\log B - \log A}{\log C - \log A} = \frac{b - a}{c - a} \qquad (3)$$

where areas A and B are non-overlapping portions of area C, such that B is greater than A, and the number of species of these areas are *a*, *b*, and *c* respectively.[236] Thus if the number of species in the two study areas *A* and *B* be determined by direct observation [*A* was generally a single quadrat, *B* a hundred quadrats], then the number of species to be found in any larger area *C*, may be calculated.

Gleason held the equation to be valid:-

> " ... as long as its use is restricted to an area of general environmental and floristic similarity, in which plants are distributed according to the laws of probability and chance, that is, to a single plant association."[237]

Whether plants are best thought of as being distributed according to the "laws of probability and chance" was, in itself, a controversial matter. However Gleason had great faith in the predictive power, to within very precise limits, of his species area formula:-

> "But the equation worked. It was never off more than 4 per cent; often less than 1 per cent. It would predict the number of dicotyledons, or the number of foreign species, or even the number of grasses or composites, just as accurately as the total of all species. It was exciting but wearisome work. The count of a hundred quadrats could easily be made in the course of an hour. Then came the bench-table work to determine the size of the area [*C* in equation 3 above]. Next came the laborious work of discovering every species on the tract. The whole area was divided off into strips about six feet wide and each strip was searched with every possible care. In a ten-acre tract, the search and the shifting of the strings separating the strips required about thirty miles of walking and might easily require three days work. As one starts this long task, the number of species grow rapidly as far as thirty or forty, then more slowly, and finally with discouraging slowness. Finally the last species is found, a little plant of Polygala paucifolia nestling in the shade of a half-rotten log, but one does not know it is the last. Sixty-four species have been discovered. Then one gets his table of logarithms and from his first results computes the number of species to be expected, 64.46, an error of less than one per cent, and is glad that he found that last little Polygala."[238]

Gleason held the fact that there was a definite mathematical relationship between number of species and area to indicate that plants were distributed by chance rather than each species having its own peculiar environmental preferences. However, he developed a further statistical test to show this more directly.

The basis of the test was as follows - if species *a* occurs in 50 quadrats out of 100, and species *b* in 50 quadrats of the same hundred, they should occur together in 25 quadrats, provided their distribution depends purely on chance. If it is determined by environmental factors, Gleason argued, the species should occur together in more than 25, if they require the same conditions, or in fewer than 25, if their demands are different.[239]

Gleason chose to display the efficacy of this test in an aspen association. Aspen forest, he wrote, "impresses the observer as offering unusually diverse environments for one association, and leads him to expect that here if anywhere species will be more or less controlled in their distribution by environmental factors."[240]

However even in the motley aspen association, Gleason was unable to identify any species or group of species whose distribution was in any way incompatible with the expectation from pure chance:-

> "In other words, environmental differences in the aspen association, while easily observable, are not of sufficient magnitude to affect the distribution of the species, unless these differences exist within the limits of a single square meter."[241]

Gleason further argued that such finely grained environmental differences were not likely to exist or be effectual. Thus he concluded:-

> "All these facts warrant the general conclusion that, within the limits of a single plant association, the environment, while possibly presenting observable differences, is essentially homogeneous for each species; that the distribution of species is primarily a matter of chance, depending on the accidents of dispersal; and the number of individuals of a species, other things being equal, is an index to its adaptation to its environment."[242]

Gleason's test for species grouping, while rough-and-ready, was the most sophisticated operation of its kind undertaken by an American ecologist up to that time, and for some time afterwards. It showed a readiness to use statistical methods to manipulate quadrat data and to interpret the nature of vegetation. Such an attitude was quite absent from the work of the majority of Gleason's contemporaries who were, first and foremost, descriptive ecologists - Cooper or

Nichols might be mentioned as examples. Clements had introduced the quadrat into ecological research but he continued to employ subjective estimation of communities as the basis of classification. Quadrats were used to describe the composition of previously-determined units, rather than as the basis of classification.

On the North American continent there had, up until then, been few attempts to describe vegetation quantitatively, beyond crude counting of the numbers of plants and species. The few American ecologists who were quantitatively minded were environmetricians, like Livingston and Shreve, concerned with measuring the physical parameters of the plant habitat. American ecologists were not, generally speaking, emulating the work being done on the continent of Europe to develop statistical techniques for the characterisation of vegetation.[244] (Such techniques were becoming an important part of the methodology of both the Uppsala and Zurich-Montpelier schools).[245]

One of the very few exceptions to this general pattern was S.A. Forbes. Forbes had published a very early attempt at a quantitative measure of species association as early as 1907, in the issue of the _Bulletin of the Illinois State Laboratory_ which contained Gleason's first ecological publication.[246] Thus Forbes must have been engaged on this statistical work at the same time as Gleason was making his first quantitative assessments of species abundance. In the twenties, Forbes's work on measuring the "associational relations of species" attracted some fresh interest and he again published in this field.[247] But his method was designed chiefly for animal populations and was technically quite different from Gleason's. Gleason's statistical ecology was, as I have said, distinctive and innovative.

Rare mathematical skills

Gleason had no formal training in mathematics beyond his freshman year at Illinois, during which he was taught algebra and trigonometry. But he was always greatly fascinated by numbers and calculations. While an undergraduate he had become interested in astronomy:-

"I had a book of spherical trigonometry which I had never studied in school, and from it learned to do all sorts of calculations such as the time of sunrise and sunset. For several consecutive weeks I charted the position of Mars against the fixed stars and from these crude observations worked out the length of its year. I missed the true figure by only a quarter of a day, but that was just bad luck ... I had become acquainted with Joel Stebbins, professor of astronomy, and used to talk to him about my problems. One of them impressed me as very simple, but I could not solve it. I saw a star rising in the east and another setting in the west and at that particular moment both were apparently the same distance above the horizon. I knew what both stars were and I could easily get their sidereal positions from the Nautical Almanac. I thought that such observations would be a good way to determine the correct time, but I could not solve the equation."[248]

This interest in figures persisted throughout his life:-

"Dr. Gleason had a strong mathematical bent, which showed in many ways ... He belonged for many years to a men's bridge club, which met on Sunday afternoons ... They would play bridge for a couple of hours, take a break for refreshments, and then play again for a couple of hours. Dr. Gleason was not formally a teetotaler, but he was abstemious, and he took nothing alcoholic on these occasions. He and one other man ... were the only ones in the party that did not indulge. Dr. Gleason kept a cumulative record of the scores over a period of years. He told me that during the first session he and his non-drinking friend were just average players, but that during the second session they were marvelously good."[249]

The younger of Gleason's two sons, Andrew Mattei Gleason, became an eminent mathematician and is now a professor of mathematics at Harvard. He very kindly provided me with the following assessment of his father's interest and abilities in mathematics:-

"Dad was not well educated in Maths. There was no question. I don't think he had ever taken a course in calculus for example. He had a very good sense of mathematics though, in a very over-the-table sort of way. So much so that he was very good at mental arithmetic. I'll tell you an amusing thing - when we were very little he had some games which we played which were dependent on various purely mathematical arithmetic tricks. One I remember particularly was that he would invite one of the kids ... to write a three-digit number down and he would thereupon immediately write another three-digit number down next to it and say 'Here take this away and divide it and you will see that it

> is divisible by 37'. He could do this with respect to several different divisors. I got very curious as to how he did this and it wasn't until I was about fourteen that I figured out how it was done. I don't know how he found out how to do this. From the point of view of a professional mathematician it is very simple but he found this out himself. There is no question that he just observed how to do this and figured out how it worked. And he could do it for several different integers as divisors - the same kind of trick. Well that was one of the various things - but then he had a number of ... little funny stories which he told ... and illustrated with numbers ... He had worked these problems ... up just because he liked to do this sort of thing. He had no real mathematical education, certainly knew nothing like as much mathematics as many freshmen. On the other hand, he was quantitatively oriented. There is no question about that. He was quantitatively oriented to the point that he used to - regularly - walking to the railroad station, he would clock himself from the back steps to such and such a telephone pole and see if he was ahead or behind his usual time - that sort of thing. He was very conscious of very detailed, quantitative thoughts about what was going on, about everything."[250]

Professor Gleason can offer no explanation for his father's interest in quantification - save that Henry Allan's own father, Henry Milton Gleason, was also interested in numbers and calculating. Despite never having been at college, he taught Henry Allan to use logarithms. Henry Allan Gleason's interest in mathematics is perhaps best thought as being simply a matter of personality. However, given that Gleason possessed such skills and interests, it is not surprising that he sought to utilise them in his professional work - to count plants and to perform statistical operations upon the data, especially since, as we have seen, with the work of Forbes and Kofoid, quantification had been part of the practice of ecological investigation in the institution at which Gleason was trained.

Although Gleason was naturally an able mathematician, he was not a technically accomplished one. He obtained the formula that bears his name (equation 1 above) by trial and error. He was unable to derive the equation formally:-

> "I wanted to discover the relation between the number of individual plants and the Frequency Index ... I need only say that I had a hard time doing it. It went easily enough for a few plants distributed over just a few quadrats. I could solve such problems on a

> piece of paper. For more plants or more quadrats I borrowed a big computing machine ... which could handle numbers up to twenty figures long. For a lot of plants or a lot of quadrats, I was still completely baffled. At last I stumbled by chance on a way to extrapolate my figures for a given number of plants or quadrats to the next higher number above. Now the computing machine could be used again for a time, but as the numbers grew larger I was stuck once more. Also in some unknown way I lost my formula and several years went by before I rediscovered it. In the meantime I had found an algebraic formula which could be worked easily, regardless of the number of plants or quadrats, merely with the help of a table of logarithms. How I ever discovered it is a mystery to me now, but I could test it out on smaller numbers and see that it worked ... Unfortunately I could not prove my formula and in my printed article I merely stated it, leaving people to think (so I hoped) that it was a very simple matter that every schoolboy and of course every ecologist ought to know."[251]

Gleason's Formula is, however, not difficult to derive from first principles. The task would not be far beyond a talented schoolboy mathematician. Gleason's son, Andrew, solved the problem in a few minutes, while a college freshman. Gleason's equation for the relationship between area and number of species (equation 3 above) was likewise arrived at entirely empirically.

Clearly, under these laborious conditions of work, Gleason's potential in mathematical ecology was necessarily limited. The mathematical exposition in his 1920 paper is cumbersome and difficult to follow. The notation is confusing. I mean by these remarks no disparagement. His contributions were certainly original and pioneering. His quantitative work shows a fine grasp of statistical problems and underlying principles.[252] But it must be seen in perspective. Gleason was not the man to transform ecology into a predominantly quantitative or mathematical discipline - even if this had been his desire. And there is no evidence that it was. Gleason was not possessed by a reforming zeal for the introduction of quantitative techniques into ecology - such as possessed many ecologists from the nineteen-fifties onwards.[253] Gleason had, on this point at least, no fundamental quarrel with the established modes of work - of which he was a skilled practitioner. He considered his quantitative work important but his advocacy of quantification was mild.[254] Gleasonian statistical ecology was a complement to observational and descriptive methods. It was not an explicit challenge to orthodox techniques in a way that, for instance, experimental taxonomy or biosystematics was a challenge to herbarium taxonomy.[255]

In the nineteen-twenties most of Gleason's colleagues were markedly less quantitatively minded or skilled than he was. David Goodall's comprehensive (but probably not quite complete) bibliography of statistical plant sociology lists only thirty-one papers published in America before 1940.[256] The vast majority of these were concerned with the testing of techniques empirically in the field; very few were concerned with developing new statistical tools in the manner demonstrated by Gleason. The few who did take up the example of his work were likewise handicapped by technical limitations:-

> "Two people in California tried in vain to solve it [Gleason's Formula] and they set up an elaborate apparatus to scatter small counters representing plants over a grid of squares representing quadrats. When they got through with this empirical test, they wrote 'Having established the truth of Gleason's Formula ... ' and went ahead with their work on actual plants."[257]

It was many years yet before circumstances were such as to bring about the large-scale introduction of mathematical techniques into ecology.

Much of the historical interpretation I offer in this chapter is predicated upon the observation that cognitive innovation tends to be structured by previously acquired skills and commitments.[258] For example, we have seen that, when called upon to do animal ecology, Gleason produced an important innovation by applying within a zoological context the techniques for the analysis of succession which he had acquired in the course of his earlier botanical work. I also sought to understand the development of his ecological perspective in terms of his applying within the context of his ecological research, skills developed in the course of his training in floristics. Likewise his mathematical skills and aptitude found expression within his ecological work.

However it is not only at the level of the individual that innovation is so structured. The adoption of a new idea or technique by a specialty as a whole, or by significant sub-groups within it, is often dependent on the proposed innovation being perceived as allowing the utilisation of skills already held by the specialty's members. Thus Cowles's physiographic exemplar was widely and readily adopted, partly at least because, in applying it, ecologists or would-be ecologists, were able to get further mileage out of skills they already possessed. Gleason's mathematical innovations, however, suffered precisely the opposite fate. They were not generally adopted because ecologists in the 1920s lacked the necessary interest in quantification and were not sufficiently mathematically sophisticated.[259]

From our present point of view, however, the interest of Gleason's mathematical ecology lies in the fact that it expressed Gleason's concept of the nature of vegetation. Firstly note that his statistics, like every other aspect of his ecological investigations, were based solely upon species as the objects of analysis. He attempted no statistical description of the plant community in terms of physiognomic types, of growth-forms, or any other non-floristic feature.

Furthermore, Gleason maintained that the species, within any given stand of vegetation, were distributed uniformly - that is, in Gleason's terms, at random. All his statistical procedures were predicated upon this assumption. He acknowledged that the environmental control of the dominant species affected the species composition of the underlayers but not, he argued, sufficiently strongly or precisely to produce detectable departures from random, within any single association. In other words, plants do not occur in co-evolved groups, each plant uniquely adapted to live with its fellow members of the co-evolved group. There is little supra-individual patterning within the plant community. For instance, Gleason offered no mechanism to explain why the distribution of species obeyed his species/area formula (equation 3 above). No such mechanism was held to apply. Species distribution was simply a matter of probability, not the result of biologically meaningful 'community functions', to use Clements's term, or 'organizing factors', to use Tansley's.[260]

Such uniformity was only relative however. On a larger scale, all was variation. A single small stand might be uniform. But no two isolated examples of the same sort of vegetation were identical. Large associations changed gradually throughout their extent. Gleason's investigations into the statistics of species distribution all served to illustrate this, to Gleason, fundamental feature of vegetation. He developed statistical tests, the purpose of which was to highlight the spatial variation of species composition - in other words to demonstrate objectively the tenets of the individualistic hypothesis.

One might say that Gleason's arguments for the existence of small-scale uniformity undermined the possibility of small, co-adapted units, units on the scale of the Continental European association; on the other hand, his statistical expression of large range variation undermined the possibility of large co-adapted units, units on the scale of the American association or formation. In other words, all his mathematical investigations expressed and supported his individualistic concept of the plant association. His floristic interests and his ecological theories structured the form in which his natural aptitude for mathematics found expression.

The vegetational history of the middle West

While at the Botanical Garden, Gleason published several papers on plant geography - both floristic and ecological. The most important of this series of papers was published in 1923. It was entitled "The Vegetational History of the Middle West".[261] An earlier version had been written while Gleason was at Michigan but he had experienced some trouble in getting it published.[262] Eventually, on the recommendations of Cowles and Transeau, it was accepted for the Annals of the Association of American Geographers.[263] The paper is interesting for in it Gleason combined the dynamic viewpoint of physiographic ecology with the longer historical perspective afforded by floristic phytogeography. Gleason's vegetational history drew, thus, upon both his ecological and his floristic skills. The combination well illustrates the amphibious nature of Gleason's research interests.

European floristic phytogeographers had long been interested in elucidating the history of present-day plant distribution - by locating the geographical point of origin of species, genera and flora and following their subsequent migrations. In the 1900s, as we have seen, C.C. Adams introduced this European historical perspective into the investigation of the flora and fauna of the Middle West.[264] But his example had not led to much further work - until it was taken up by Gleason.[265] In the 1923 paper Gleason applied Adams's historical model and sought further to improve historical phytogeography by incorporating within it an ecologist's understanding of such matters as succession, associational migration, the environmental requirements of species, the continuity of habitats, and the significance of relic plant communities. And returning to matters he had first discussed in his Master's thesis, Gleason sought to demonstrate that light could also be shed in the opposite direction - the ecologists' understanding of vegetation could be enhanced by a consideration of floristics and floristic history.

Previous attempts at interpreting the history of vegetation in the United States had been based upon backward extrapolations of present-day successions, and, in Clements's case, upon the reconstructions of the climates of the past.[266] From Gleason's point of view, the former technique could only give a partial picture of the history of vegetation, since the displacement of one climatic climax by another might bear little similarity to physiographic succession - even assuming present-day successions could be reliably extrapolated backward in this way. (Gleason had already argued they could not.)[267] Clements's study of climatic changes also seemed to be limited in that it was based almost entirely upon the evidence provided by the physiognomic types of fossil plants and upon a cyclical theory of climatic change. Gleason however sought to extrapolate the dynamic viewpoint into the history of vegetation, not simply in terms of present-day successions, climatic changes or fossil physiognomies, but by incorporating what was known or could be deduced about the migration and evolution of species and floristic elements.

Drawing upon both his ecological and his floristic skills, Gleason was thus able to provide simultaneously a history of the floristic elements and of the vegetation-types of the Middle West. His combination of ecology and historical phytogeography was remarkably fruitful. He mustered evidence from both fields with great skill and constructed a grand and plausible vision of vegetation-types advancing and retreating over the plains as climatic and topographic changes occurred. His most notable success lay in the postulation of a xerothermic - mild and dry - climate, existing in the Middle West immediately after the Wisconsin period of glaciation. This had been accompanied by a large eastward extension of the prairie, Gleason argued. The existence of such a xerothermic period was intensely controversial for some time, but was later corroborated by fossil palynology.[268]

Given the paper's great originality, it is perhaps not altogether surprising that Gleason initially had difficulties in getting it published. American phytogeographers had not followed Adams's advice to introduce the historical perspective into the subject. And American ecologists had been antipathetic toward floristic studies, for as long as there had been ecologists in America. As Raup put it:-

> "A striking corollary to the development of physiological plant geography has been its antipathy toward floristic ideas. This has been particularly true in America ... Floristic geography was regarded as primitive and outmoded useful only for the mass of facts it accumulated."[269]

Shreve, for instance, maintained that:-

> "The physiological phase of the study of the plant life of particular areas, Ecological Plant Geography, is not at all concerned with the systematic relationships of plants but rather with their form, structure, and functions, and the relation which these have to the physical and organic environment of the individuals."[270]

Arguing from a somewhat different perspective, Cowles likewise regarded orthodox taxonomy practice as being of only secondary importance:-

> "No one realizes so well as does the ecologist the inadequacy of laboratory experimentation in the settlement of field problems. The ecologist feels that the species problem is essentially a field problem and hence incapable of final settlement either in the

herbarium or the laboratory ... One of the noblest aims of ecology is the destruction of many of the species of our manuals. Where the critical study of species is confined to the herbarium, it often happens that ecological varieties or habitat forms are given specific rank."[271]

Cowles concluded:-

"It is to be hoped that the taxonomists and particularly those taxonomists who have sinned in the much making of species and those who made a so-called critical study of plants without any adequate training in the general principles of botany, will reform their ways. In truth they must reform ... Taxonomy must be scientific. It must require for its devotees a training as rigid as that required by professional workers in morphology, physiology or ecology ... If the taxonomists of the future fail in these respects a hard but certain fate awaits them. The world of morphologists, physiologists and ecologists has borne with them patiently and long and has deferentially abided by the specific determinations of taxonomists ... These things will not be endured much longer; a little more and the sinning taxonomists will be "cast out into the outer darkness where there shall be wailing and gnashing of teeth"."[272]

As we saw in the previous chapter, Clements also had a low opinion of the usefulness of floristic botany as then practised in North America.[273]

Gleason was thus one of the very few botanists who took both ecology and floristics seriously. This dual commitment had a formative influence on his interpretation of vegetation. The fact that he had a foot in more than one botanical camp explains much of the content of Gleason's work. It also helps elucidate the reception of some of Gleason's work by his colleagues. As far as the publication of his "Vegetational History of the Middle West" is concerned, one might say that having a foot in both camps almost caused him to fall between two stools.

The individualistic concept revisited

During the nineteen-twenties Gleason's duties at the Garden did not prevent him undertaking further ecological field research. In 1924 he investigated the composition and successional relations of some of the few tracts of virgin deciduous forest left in the northern part of the Lower Peninsula of Michigan. The results of the study, with general remarks on the structure of the maple-beech association, were published the following year.[274]

And in 1925, at the instigation of Melville Cook, a plant pathologist employed at the Insular Experiment Station in Puerto Rico, Gleason was invited by the Puerto Rican authorities to undertake an ecological survey of the island. Gleason spent three months there in 1926, on paid leave from the Garden. This greatly increased his acquaintance with exotic vegetation. The report, with Cook as co-author, appeared early in 1927.[275] This visit to Puerto Rico was however to be Gleason's last major ecological field trip.

Undoubtedly the most important piece of ecological work that Gleason produced in the Twenties was a re-expression and amplification of his individualistic concept of the plant association. This was published in 1926.[276] In the introduction to this article Gleason pointed to the continuing failure of ecological investigators, on both sides of the Atlantic, to achieve any general agreement as to the fundamental nature and classification of plant associations. Such chronic disagreement "leads one", Gleason wrote, "to the suspicion that possibly many of them are somewhat mistaken in their concepts or are attacking the problem from the wrong angle".[277] Gleason made it explicit that his quarrel was not only with Clements. He invited all plant ecologists to abandon their "pre-conceived ideas" as to the nature of the plant community:-

> " ... we may conclude that we would better demolish our whole system of arrangement and classification and start anew with better hope of success ... Is it not conceivable that, as the study of plant associations has progressed from its originally simple condition into its present highly organized and complex state, we have attempted to arrange all our facts in accordance with older ideas, and have come as a result into a tangle of conflicting ideas and theories?"[278]

Gleason was thus posing a radical challenge to the basis of contemporary practice in the study of plant communities.

Gleason acknowledged that plant associations existed and might be recognised on the ground. The ecologist in the field frequently came across areas of vegetation which were uniform, to the extent that any two small subdivisions of the vegetation appeared quite similar. Such areas were conventionally designated 'associations':-

> " ... but different ecologists may disagree on a number of matters connected with such an apparently simple condition. More careful examination of one of these areas, especially when conducted by some statistical method, will show that the uniformity is only a matter of degree, and that two sample quadrats with precisely the same structure can scarcely be discovered. Consequently an area of vegetation which one ecologist regards as a single association may by another be considered as a mosaic or mixture of several, depending on their individual differences in definition."[279]

There was no general agreement among ecologists as to how much variation ought to be included within a single association.

Gleason admitted that, in northern latitudes, a technique of delimitation based on the identification of character-species - species or sets of species limited to single associations - had had some success.[280] But the success of this technique, Gleason claimed, was dependent upon the flora of these regions being especially impoverished. In other areas such a system would not necessarily be efficacious. Here Gleason drew on his experience of vegetation outwith the United States:-

> " ... in many parts of the tropics, where diversity of environment has been reduced to a minimum by the practical completion of most physiographic processes and ... where the flora is extraordinarily rich in species, such a procedure is impracticable or even impossible. Where a single hectare may contain a hundred species of trees, not one of which can be found in an adjacent hectare, where a hundred quadrats may never exhibit the same herbaceous species twice, it is obvious that the method of characteristic species is difficult or impracticable." [281]

This account of the floristic richness of the tropical forest mirrors quite closely his description of the Makiling forest, quoted earlier. Gleason was thus the first, as far as I am aware, of a series of investigators who were to argue, most vocally in the late fifties, that the concept of the plant association would not have arisen if tropical rather than temperate vegetation had been the first to be studied.[282] Doubtless Gleason's trip to the tropics helped nurture and sustain his confidence in his individualistic view.

Gleason argued that the floristic aspects of the vegetation did not allow the universal identification of precise associational boundaries. Nor could the features of the physical environment provide the basis for a foolproof definition of the association. Different environments supported similar communities; similar environments, different ones. All in all, it must be concluded that associations were not necessarily delimited by distinct natural boundaries.

Gleason then introduced the argument that was to attract most attention in the post-war years. He argued that associations did not repeat themselves exactly but rather that vegetation consisted of a continuum of variation:-

> "A great deal has been said of the repetition of associations on different stations over a considerable area. This phenomenon is striking indeed, and upon it depend our numerous attempts to classify associations into larger groups. In a region of numerous glacial lakes, as in parts of our northeastern states, we find lake after lake surrounded by apparently the same communities, each of them with essentially the same array of species in the same numerical proportions ... But even this idea, if carried too far afield, is found to be far from universal. If our study of glacial lakes is extended to a long series, stretching from Maine past the Great Lakes and far west into Saskatchewan, a very gradual but nevertheless apparent geographical diversity becomes evident so that the westernmost and easternmost members of the series ... are so different floristically that they would scarcely be regarded as members of the same association."[283]

Similarly, along the floodplain of the Mississippi, the forest seems constant in composition for mile upon mile. But as:-

> " ... the observer continues his studies further downstream, additional species very gradually appear, and many of the original ones likewise very gradually disappear. In any short distance these differences are so minute as to be negligible, but they are cumulative and result in an almost complete change in the flora after several hundred miles. No ecologist would refer the alluvial forests of the upper and lower Mississippi to the same associations, yet there is no place along their whole range where one can logically mark the boundary between them. One association merges gradually into the next without any apparent transition zone."[284]

Ecologists, who necessarily tended to limit their field research to relatively small study areas, seldom recognised such continuous variation in space. But, Gleason argued, it was a universal feature of vegetation. Simple statistical analysis would corroborate that isolated associations did not repeat themselves exactly and contiguous associations might grade into one another over long distances.

Gleason then rehearsed and amplified the arguments, first expressed in 1917, that provided the theoretical underpinning for his rejection of the community-unit theory. No two plants were physiologically identical. Groups of species happened to grow together only because their physiological requirements happen to coincide to the extent of allowing them to utilise a particular place at a particular time. Such joint utilisation was also dependent upon the individualistic vicissitudes of migration.

The concern of the physiographic ecologists with the study of development had led many to classify successional stages together into unit-successions or series. Thus, a regular series of successional stages were held to lead through to a particular pre-determined end point. But Gleason argued that succession, like all other community phenomena, is dependent on the behaviour of the individual plants, and upon pure chance. The various stages in a successional series need not follow one another in a fixed sequence:-

> "The next vegetation will depend entirely on the nature of the immigration which takes place in the particular period when environmental changes reaches the critical stage. Who can predict the future for any of the little ponds considered above? In one, as the bottom silts up, the chance migration of willow seeds will produce a willow thicket, in a second a thicket of Cephalanthus may develop, while a third, which happens to get no shrubby immigrants, may be converted into a miniature meadow of Calamagrostis canadensis."[285]

No integrative processes operate at the level of the community:-

> "The plant individual shows no physiological response to geographical location or to surrounding vegetation per se ... "[286]

Every species of plant was best thought of as a law unto itself. The behaviour of plant species provided no basis for the segregation of definite communities:-

> "It is small wonder that there is conflict and confusion in the definition and classification of plant communities. Surely our belief in the integrity of the association and the sanctity of the association-concept must be severely shaken. Are we not justified in coming to the general conclusion ... that an association is not an organism, scarcely even a vegetational unit, but merely a co-incidence?"[287]

Why the individualistic concept?

In order to appreciate fully the implication of Gleason's apostasy over the reality of the vegetation-units, one must be aware of how deeply the community-unit theory was embedded in the practice of American ecology. The assumption that vegetation has a unit structure is, for example, quite explicit in Clements's work:-

> "The developmental study of vegetation necessarily rests upon the assumption that the unit of climax formation is an organic entity."[288]

To take a further example, in the major textbook Clements wrote with Weaver we find the following:-

> "Vegetation, like all organisms, not only undergoes development but also possesses structure. The vegetation of a continent, such as North America, is not uniform throughout. Depending upon climate, it is differentiated into large natural units such as forest, chaparral, grassland, tundra, etc. The composition or structure of each type differs from the others. Each of these larger units of vegetation is called a plant formation."[289]

Even Cooper, who frequently emphasised the changeability and variability of vegetation and who differed markedly from Clements as to the level of integration with which the community-units should be credited, likewise saw the unit of vegetation as the essential basis of ecological study:-

> "It seems to me that plant communities exist, that they are definable and comparable and therefore constitute a legitimate field of study. Naturally they are not so sharply defined as individual organisms and I cannot follow Clements and his disciples in considering them as strictly comparable. Doubtless tropical communities are even less distinct than those of temperate regions but I feel strongly that they exist."[290]

The identification of natural units of vegetation was a central component of the practice of most American ecologists. As Stanley Cain put it:-

> "For them [plant ecologists and geographers] it is the *sine qua non* of their science."[291]

As well as providing ecologists with practical tasks to do in the field and at their desks, the community-unit theory constituted an autonomous reality - of vegetation *per se* - for the would-be autonomous discipline of ecology to investigate. Study of the vegetation at the level of the community-unit had been a distinctive feature of ecological botany since its beginnings within Humboldtian science. The community-unit theory defined a unique and peculiar field for ecological study - thus helping to distinguish ecology from other branches of botany, and to re-inforcing its claim to be a discipline in its own right.

Why then did Gleason, although a dedicated ecological investigator, choose to view the plant association in an altogether different manner? I would argue that part of the explanation lies in his twin commitment to floristic botany. Gleason, as we have seen, straddled the important professional divide between ecology and taxonomy. The doing of ecological research was not his entire professional life as a botanist. Therefore the establishment of a uniquely ecological form of inquiry to emphasise the distinctive nature of the ecological specialty was not such an important matter to him as it was to botanists committed solely to ecology. To Gleason, therefore, it was not so essential emphatically to separate the two research activities. Therefore it is understandable that he should have had a lesser commitment to the community-unit theory - and therefore been prepared to countenance alternatives to it.

The appeal of possible alternatives was, no doubt, increased by the fact that the majority of Gleason's fellow ecologists generally disparaged the floristic aspects of botany in the course of their employment of the community-unit theory. American ecologists generally sought to associate themselves with the New Botany, as exemplified by physiology and morphology. Floristics was to them part of the old Botany - from which they wished to distinguish themselves. Thus Clements and Cowles laboured to reform taxonomy in the light of ecological principles and to establish the superior knowledge claims of ecology. The employment of a classification system based on a unit unique to ecology - the supra-individual community-unit - aided these claims. The autonomous ecological form of inquiry investigated an autonomous reality consisting of vegetation per se rather than simply individual plants and their species - the subjects of floristic study. As made explicit by Clements and Nichols floristic criteria were to be of secondary importance, at least in theory, in the determination of natural units of vegetation. Distinctively ecological, that is habitat, criteria were to be employed to identify the distinctively ecological unit.[292]

Gleason, however, was an extremely skilled taxonomic botanist. He had had considerable experience in floristic botany before he began his ecological research. Given these investments of skill and training, it is not surprising that throughout his career he placed a much higher value on floristic study than did the majority of his fellow ecologists. Gleason, with considerable and continuing professional investment in both floristics and ecology, did not seek to separate the two or denigrate the importance of the former. On the contrary, he emphasised the importance of floristic background for ecologists:-

> "I appeared on its [the Michigan Biological Station] staff in 1911 ... Again my previous experience was greatly to my advantage. I had learned the northern plants during my summer in Isle Royale ... and for the first time in its three years the station had a botanist who knew the flora in advance. It must have been a great strain on Burns who taught there in 1909, and on Pool, of 1910, to teach ecology without knowing the species and the students must have discovered the circumstances very promptly."[293]

And he also argued for the utility of ecology for floristics as evidenced both by his "Vegetational History of the Middle West" and by his study of the evolution and distribution of the Vernonia.[294]

Given Gleason's commitment to floristics it is not surprising that he, contra Clements and Nichols, emphasised species composition as the most fundamental feature of plant communities. All the non-floristic characteristics such as physiognomy were secondary, as far as Gleason was concerned. They were the product of the species composition - not independent features of the vegetation. Therefore uniformity of physiognomy could never be accepted by Gleason as proof of the underlying unity of any two pieces of vegetation if their species compositions were disparate. He also rejected the physiognomic synusiae theory of the Estonian botanist Lippma which had briefly had some following in the United States.[295] Likewise the study of the characteristics of the physical environment could not by itself be a primary means toward an understanding of vegetation. We have seen that Gleason expressed this point of view in his criticism both of Clements's classification of vegetation by habitat and of Fuller's evaporation theory of the cause of plant succession.

A floristic approach entailed giving primacy to the study of the individual plants and their species. This was the essence of the individualistic concept. All the phenomena of vegetation were dependent on the individual plant. The autonomous unit of vegetation, on which most ecological practice was based, did not exist. Plants, not plant communities, were the legitimate level of inquiry. Thus, Gleason's commitment to a floristic form of botanical practice must be taken as part of the explanation for his development of the individualistic concept of the plant association.

Gleason had special skills which enabled him to undertake ecological investigation at the level of the individual plant species, readily and successfully. Not only was he well trained in the identification and classification of plants, he was also extremely good at the difficult task of finding rare species in the field. Gleason's elder son, Henry Allan Jnr., trained as a professional botanist and he took a keen interest in his father's work. Professor Gleason was kind enough to provide me with the following assessment of his father's field skills:-

> "He was a meticulously careful observer. He saw things that experienced field workers passed. In 1933 he and I spent a summer collecting around the University of Michigan Biological Station. At that time that was, without question, the area that was floristically best known in all of North America. Gates was teaching ecology there, from Michigan, and had taught systematic

> botany there for years and years - a very careful field worker and he had just combed that place and it had got to the point where they were finding two or three new species a year and that was it. Well we found a couple of dozen ... The one that I think upset them more than anything else was - Nuphar advena the common yellow water lily, it grows all over there, they came across it all the time ... We just got to looking inside it and we found - right on Douglas Lake - the lake that they went on all the time - we found Nuphar rubrodiscum. At a distance the things look exactly alike but when you look inside the big disc at the top of the stigma is red instead of yellow. And so it went ... We looked at plants more closely than people had looked at them ... that was one of his peculiarities ... that kind of observation."[296]

Thus Gleason's advocacy of a floristic, individualistic approach to vegetation correlated with his possession of all the various skills of a first-rate floristic field botanist - whose practice was necessarily based upon the individual plant and its species.

However, by arguing that Gleason held a fundamentally floristic view of vegetation, I do not mean to disparage his understanding of the dynamic processes of vegetation. Gleason's published work clearly illustrates that his approach to vegetation was as dynamic and comprehensive as either Clements's or Cowles's. To Gleason, the floristic study of plant communities was not an end in itself:-

> "I used to tell my students flatly that the plants they got acquainted with in taxonomy might never be seen again, unless they lived or taught school in this same north country; that the plant associations to which I introduced them in ecology were also northern. I wanted them to learn how to recognize an association, how to write a clear and reasonable description of it, how to discover its successional relation to neighboring associations, and so on. If they developed that skill, then they could do ecological work anywhere."[297]

But, to Gleason, dynamic properties of vegetation, such as successional change, were the product of the action of individual plants - not attributes of the plant community as a collective entity. Thus general principles governing the behaviour of vegetation as a whole could only be discerned by investigation at the level of the individual plants. Studies of migration, of spatial and temporal variations in species composition, and other individualistic features were not, as I have said, ends in themselves - but they were the primary means whereby Gleason sought to investigate and understand vegetation.

Gleason's commitment to floristic botany structured his ecological practice - in such a way that his floristic competences could be maximally utilised within his ecological investigations. And the individualistic concept of the plant association provided a theoretical legitimation of the practical connection Gleason wished to make between floristics and ecology. The individualistic concept created a formal cognitive framework for ecology, within which floristic skills were necessarily to be allowed full expression. It sanctioned the primary role which Gleason granted floristics in the making of valid ecological knowledge. It entailed that no other form of expertise, whether physiological, geomorphological or physical, could take precedence over the expertise possessed by the floristic botanist.

The floristic character of Gleason's individualistic concept of the plant association exemplifies a pattern of cognitive construction, well known to sociologists of science. Pre-existing competences and practices are brought to bear on new problems - thus structuring cognitive innovation around prior investments of skill and training.[298] As Gleason put it:- "My first research was in taxonomy."[299] This early training in taxonomy structured his approach to ecological processes and phenomena. Such a perspective was maintained by his continued involvement in floristic research.

Gleason's distinction from other 'individualistic' ecologists

That Gleason's perspective on vegetation was at least partly the product of his background in floristic botany helps us also to understand how and why he differed from some other contemporary botanists - in particular those who recently have also been identified as having had individualistic views. For instance, McIntosh and Billings have drawn attention to apparently Gleason-like individualistic statements made by the physiological ecologists, Livingston and Shreve.[300] Certainly these ecologists stressed, as Gleason did, that vegetation ought to be approached in terms of its individual component plants:-

> " ... we have tried to bear constantly in mind the conception that vegetational characters are simply the expressions of the activities of individual plants."[301]

They did not admit the possibility of 'special laws' of 'mass action'.[302]

Furthermore, Livingston and Shreve argued that no two plant species were quite identical in their habitat requirement, and hence no two plant species had identical patterns of distribution. As Shreve had written in 1914:-

> "It is impossible to study the distribution of vegetation in a region where pronounced differences may be found within short distances without being impressed with the independence which each species exhibits in its allocation ... It is nowhere possible to pick out a group of plants which may be thought of as associates without being able to find other localities in which the association has been dissolved ... The physical requirements of plants are so varied and so elastic that the composition of a series of communities occupying similar habitats in widely separated places shows the constant overlapping of the ranges of individual species which is due to the physiological inequivalence of these species."[303]

However, as well as these striking similarities there are also important differences to be detected between Shreve and Livingston on the one hand, and Gleason on the other. For instance, Shreve and Livingston had little sympathy with the aims of floristic botany:-

> "The study of vegetation <u>as such</u> has been, on the whole, greatly obscured by the fact that it has never been completely divorced from the study of the flora. Too much emphasis cannot be laid, at the present time, on the radical distinctness of the work of physiological plant geography, on the one hand, which attempts to relate the occurrence and distribution of species as physiological entities, to the factors of environment, and the work of floristic plant geography, or phyto-geography, on the other hand - which attempts to reveal the geological history, the movements, and vicissitudes of species as phylogenetic entities. The floristic flavor which plant geography and ecology have always possessed may be largely accounted for by the fact that all plant-geographical interest has sprung historically out of floristics, and by the fact that we are in the position of not being able to mention a plant of particular identity without using its technical Latin name, which is solely an abbreviated expression for denoting the place we believe it to occupy in the phylogenetic scheme ... Nevertheless, in order to come

squarely to face with the problems of physiological plant geography, we shall have to lay aside much that floristics has taught us, and shall have to ignore phylogeny, except in so far as it shows us that plants of close kinship often have the same or similar anatomical and physiological characteristics."[304]

Livingston and Shreve were thus dismissive of research practices which were, as we have seen, extremely important to Gleason. They did not share the interests which shaped the "Vegetational History of the Middle West". The difference in attitudes to floristic botany correlates with the fact that neither Shreve nor Livingston had any particular training or experience in taxonomic or floristic botany.[305] Livingston did gather together a small private herbarium while at high school but, as he put it:-

"I never received any instruction in systematic or taxonomic botany anywhere except in the half-year course in high school."[306]

However, as an undergraduate at Illinois, Livingston had had an extensive training in physiology. This was before he developed a professional research interest in ecology:-

" ... I asked Prof. F.C. Newcombe to let me take his lectures in plant physiology, omitting the laboratory work, but he said that would be only a half-year course and it would do me no harm to know a bit about physiological experimentation; furthermore, he would predict that after I had completed that laboratory course I would find physiology more interesting than any other field of botany. How he reached that prediction I can't tell, but I became his laboratory assistant the next year, and have stuck to physiology ever since. Newcombe was not interested in ecology, which was then just getting started under the leadership of Warming and Schimper. Their books were not available to me till I went to the University of Chicago in the summer of 1897. I was a confirmed enthusiast for physiology by then."[307]

Livingston therefore came into ecology with an established interest in physiology rather than in floristic botany. It is not surprising therefore that his approach to ecological problems was a physiological one:-

"Our attitude towards plants has been that of the physiologist ... "[308]

This entailed an individualistic viewpoint in the sense that the distribution of plants was correlated with each plant's distinctive physiological capabilities, as demonstrated by experiment in the laboratory, or inferred by observation in the field. The distribution of vegetation was, to Livingston and Shreve, the product of the distribution patterns of the individual plants. The fundamental rationale behind this physiological approach lies in the premise that the majority of plants have their distribution controlled directly by the physical environment:-

> "The great bulk of the trees, shrubs, grasses, root-perennials, and other plants which make up the dominant natural vegetation of the world may safely be held to have had their present distributional limits imposed by physical factors which are either now operative or were operative in very recent time."[309]

The identification of which physical factor controlled the distribution of which species was the principal research goal to which Livingston and Shreve's activities were directed.[310]

Such concern with the physical environment led Livingston and Shreve to place rather less emphasis than some of their contemporaries upon vegetational dynamics. There is, for instance, no discussion of succession whatsoever in Shreve's book-length study of the vegetation of the Santa Catilina mountains of southeastern Arizona.[311] Plant succession was not a very interesting topic since it shed little light on the mechanisms of environmental control:-

> "As soon as we begin to study the relation of physical conditions to successional stages, the relation of these stages to each other sinks to a position of minor importance, and our work emerges upon the broad field of causational plant geography."[312]

Shreve, in his study of the montane rain forest of Jamaica, similarly argued that processes of succession were important only as they were reducible to the effect of the physical environment:-

> "Any successional phenomena which might be discoverable in the montane rain-forests, whether due to such physiographic change as the merging of a maturing ravine into its mother slope or to such climatic change as would cause a relict alpine meadow to be invaded by forest, would in any case resolve themselves into a matter of the gradual change of vegetation in dependence upon a gradual change of physical environment. The relation of the old vegetation to its environmental conditions,

> and the relation of the succeeding vegetation to its environmental complex are both matters that would far outweigh in importance the floristic and ecological features of the succession itself."[313]

In the atmometer work discussed earlier we saw another attempt to interpret succession not in vegetational but in physical terms.

But Gleason was unlikely to accept this subordination of vegetational dynamics to physiology. Much of his field practice consisted of attempting to explain vegetational change in 'floristic and ecological' terms. And his individualistic concept did not diminish the importance of processes such as succession. In 1927, he published a major theoretical paper on the 'succession concept' - in which he elaborated how successional change could be understood in the light of the individualistic concept and indicated the advantages to be gained from this re-interpretation.[314]

Gleason sought to understand vegetational dynamics in individualistic terms. But the centrality of vegetational change within the research programme of dynamic ecology would not be thereby altered. The study of succession as a vegetational process was still an important element of practice. Gleason's individualistic concept of the plant association therefore functioned, broadly speaking, within the general context of physiographic ecology. Livingston's and Shreve's physiological individualism was, on the other hand, outwith that context. It belonged to physiological ecology - the other great division of early American plant ecology. In this research programme, vegetational processes were not themselves explanatory categories, nor were they the primary objects of field research. 'Floristic and ecological features' were to be reduced to the more fundamental (from this point of view) explanatory level of physical and physiological variables.

Given these differences between physiographic and physiological plant ecology, together with the more specific, but just as significant, divergence in attitude between Gleason on the one hand, and Livingston and Shreve on the other, as to the importance of floristic botany, it is not altogether surprising that Gleason, Shreve and Livingston never made common cause. Nor is it surprising that the apparent similarities between their 'individualistic' theories were not recognised by their contemporaries.[315]

The Ithaca Conference, 1926

The fact that Gleason's practice lay nearer physiographic than physiological ecology did not however entail the general acceptance of his work by the physiographic ecologists. His ideas certainly belonged to physiographic ecology, but they were controversial within that context.

The publication of Gleason's second (1926) paper on his individualistic concept caused an immediate reaction among ecologists. An entire half-day session of the Ecology Section of the International Congress of Plant Sciences was set aside in order to discuss it. The Congress met in August 1926. Nichols, who was then Chairman of the Ecology Section, took the opportunity to present a paper detailing his objections to the arguments put forward by Gleason.[316] He allowed Gleason to read his paper before it was delivered and Gleason was able to prepare a reply.[317]

Interestingly the first polemical tactic adopted by Nichols in his criticism of Gleason was not the presentation of substantive counter-arguments. Rather he chose to point to the general consensus among ecologists that, contra Gleason, definite units of vegetation did exist - and to emphasise the centrality of such a conception of the plant association within the normal practice of the specialty:-

> "But those ecologists are few and far between who would not recognise the plant association concept as something which is at least susceptible to more or less definite characterisation. ... By some ecologists, the term association is applied to the concrete pieces of vegetation which we study in the field and which correspond to the individual plants of the taxonomist. By others, these individual pieces of vegetation are regarded merely as examples of an association, in much the same way that different individual plants of the same kind may be regarded as examples of a particular species. By many, the term association is applied in both (or in all three) of these senses." [318]

It was as if Nichols was reminding his audience of the vested interest they had in the theoretical status quo - the collective commitment to the reality of community-units:-

"These, then, are the concepts of the plant association which Dr. Gleason holds up to criticism - the concepts by which we recognise vegetation as being built up of a series of vegetation-units comparable, in a way, with species ... These are the concepts which he would supplant with his own so-called 'individualistic concept' of the plant association."[319]

Furthermore, Nichols pointed out that the theoretical position which he had himself espoused in earlier papers "meets with favour among the majority of American ecologists and not a few European".[320] Thus, he presented his credentials to speak on behalf of the discipline. He showed he was well-qualified for the task of reminding his audience how Gleason's view threatened their professional interests.

The tactic adopted here by Nichols occurs quite commonly in scientific debates. A protagonist addressing the faithful, of which he wishes to be considered an accredited member, publicly delimits and defines the communalities of the group. He reminds his audience what their normal practice is, in other words where their professional vested interests lie. It might be said that he erects a symbolic totem or standard around which the tribe may rally. Such preaching to the converted strengthens the zeal and cohesion of the group and renders it easier to identify and exclude non-members. Anyone who will not rally to the standard is an outsider - not a proper member of the group - and thus may be discredited.[321]

That Nichols should adopt this mode of defence against Gleason is good evidence for my earlier point that the idea of the community-unit was central to the contemporary practice of American ecology. And thus Gleason's individualistic theorising, denying the reality of the community-unit, constituted a challenge to that practice.

Nichols conceded the point Gleason had made in the 1926 paper that there was much disagreement between ecologists as to how the vegetation-unit should be conceived. This, he admitted, was regrettable. But he stressed that there was a consensus that such units did in fact exist, however they were to be conceived. And ecology was not alone in being riven by disputes. Similar disagreements existed in the field that Gleason had now made his primary profession:-

" ... there are wide differences of opinion among ecologists when it comes to the precise definition of the term plant association; but so also are there differences of opinion among taxonomists when it comes to the precise definition of the term species."[322]

Nichols returned to this comparison between the practice of ecology and that of taxonomy again and again in the course of his talk. He repeatedly made an analogy between the plant association and the species - maintaining that the reality of the plant association was as fundamental to the activities of ecologists as the reality of species was to the activities of taxonomists - notwithstanding the disputes in both disciplines as to the exact definition of each concept:-

"Is not the situation here identical with that faced by taxonomists, one of whom would differentiate into several species what another would treat as a single one? Is the absence of general agreement in the matter of allowable variation any more reason for discarding our concept of the association as a vegetation unit than it is for discarding that of the species as a floristic unit?"[323]

Thus, as far as being riven by "constant disagreement" was concerned, the taxonomic pot was as black as the ecological kettle. The fact that there were many taxonomists in the audience, most of whom sided with Gleason as being one of their own men, no doubt added piquancy to these remarks - especially in the context of a conference which had already been riven by disputes between taxonomists and ecologists over the species question, a matter we have already seen was the cause of enmity between the members of the two specialties.

It is worth briefly digressing from the description of Nichols's paper to outline the nature of this other Ithaca dispute, for it aptly illustrates the professional divisions between ecology and taxonomy which were current in the twenties and which Nichols sought now to exploit.

In 1923, Harvey Hall and F.E. Clements, colleagues in the employ of the Carnegie Institution at Pike's Peak, published The Phylogenetic Method in Taxonomy.[324] The book contained much criticism of orthodox taxonomic procedures and urged the adoption of experimental methods. Clements returned to criticisms he had made in 1905:-

"The thought of subjecting forms presumed to be species to conclusive test by experiment has apparently not even occurred to descriptive botanists as yet. Notwithstanding there can be no serious doubt that the existing practice of resplitting hairs must come to an end sooner or later. The remedy will come from without through the application of experimental methods in the hands of the ecologist and the cataloguing of slight and unrelated differences will yield to an ordered taxonomy."[325]

Clements and Hall had revised the North American species of Artemsia, Chrysothamnus and Atriplex along 'phylogenetic' lines. At the Ithaca conference, Hall presented a paper outlining some of their methods. A half-day session was given over to a discussion of Hall and Clements's work.

One of the taxonomists whose work was most directly contradicted in The Phylogenetic Method was Per Rydberg, a colleague of Gleason at the New York Botanical Garden. Rydberg took the opportunity of the Ithaca conference to reply. His annoyance at having his work interfered with by an ecologist was evident:-

"That the "endless" splitting of genera and species should meet objection especially among non-taxonomists was natural. These objections have been voiced in this country, at least in print, strongest by some of the leading ecologists. The objections might have been warranted, but they should not have been presented in an over-bearing and sarcastic way. How can ecologists teach taxonomists the way to do their work? One of the former [Clements] undertook such a thing and for the purpose roped in one of our best taxonomists [Hall] to help him and the result was the publication of the "Phylogenetic Method" ... If this paper was intended as a review of the publication, I would give a good deal of praise to the main part of it. The credit is due chiefly to Dr. Hall. It is the purpose and the principle laid down in the preface that I object to, and the inconsistency in carrying out the plan. The preface was written principally by Dr. Clements."[326]

Rydberg did not confine his criticism solely to Clements and laid about ecologists as a whole for their unhelpful and inconsistent attitude to the creation of species by taxonomists. However, Hall, confident and a fine platform speaker, was held to have carried the day for experimental ecology, cytology and genetics against orthodox taxonomy.[327] For the taxonomists, however, this was only a set-back in a long campaign.[328]

To return to Nichols's criticism of Gleason - the first substantive argument he produced was on the matter of the floristic diversity of the tropical forest. But it too hinged on the question of credibility. Nichols reported that he had corresponded with two of the very few other American ecologists with experience of the tropics, H.N. Whitford and N.L. Shantz. Both these men were adherents of the community-unit theory - Whitford had been a student of Cowles and Shantz of Weaver.[329] Nichols had elicited their opinion as to Gleason's claim that, in the rain forest, definite associations could not be discerned. Both Whitford and Shantz maintained that Gleason had grossly over-estimated the variety of species composition which existed in the tropical forest. Furthermore character-species could indeed be found there; associations determined:-

> "To the average botanist, entering the tropical forest" concludes Dr. Whitford, "all seems confusion", and yet "with a knowledge of the species and quantitative studies of the composition, tropical forests can be classified by associations and can be designated by the generic and sometimes the specific names of the predominating trees."[330]

In other words, Gleason's acquaintance with the tropical forest had been too slight to permit him to make generalisations about its character. He could not be regarded as an accredited tropical ecologist. Nichols took care to point out that, by contrast, Whitford's credentials in this respect were impeccable:-

> " ... probably no American ecologist is more familiar, from actual experience, with the forests of the tropics."[331]

Nichols then addressed Gleason's arguments that it was not always possible to define the geographical boundaries of an association and that associations gradually blended into one another over long distances. These were however, to Nichols, relatively unimportant observations, with little bearing on the reality of the association:-

> "Reverting to our analogy between the association concept and that of the species, is not a piece of vegetation which comprises a mixture of the characteristics of two associations quite comparable to a plant which exhibits a mixture of the characteristics of two species? If we refuse to recognize the plant association as a vegetation unit on this account, are we not almost equally justified in refusing to recognize the species as a floristic unit because of the existence of hybrids?"[332]

Having dismissed several other of Gleason's arguments, Nichols turned to the question of the general prevalence of variation within the plant cover. Gleason held that continuous variation was universal and that this made the traditional association concept untenable. This was, to Gleason, a point of central importance. And the gradual change in character exhibited by the forests of the Mississippi flood-plain was a crucial example. However, to Nichols, the Mississippian continuum was merely a 'discrepancy':-

> "The existence of this condition no more invalidates the concept of the association as an entity or unit than does the corresponding discrepancy in taxonomic botany [individuals intermediate between species] invalidate the generally accepted concept of the species."[333]

Continuous variation was, to Nichols, the exception rather than the rule. Its existence thus did not challenge the reality of the vegetation unit.

We may discern, in these exchanges between Nichols and Gleason, a pattern frequently exhibited by scientific disputes. Different commitments produce different worlds.[334] In this present case, if one is convinced of the reality of the plant association as a natural unit, then one organises and weights vegetational phenomena in a particular manner; if one does not accept the reality of the association, then one, by contrast, arranges phenomena according to another quite different protocol. Thus what are to Gleason crucial examples may be dismissed by Nichols as relatively unimportant anomalies.[335] Throughout the exchange, Gleason and Nichols consistently failed to agree as to which pieces of evidence were to be regarded as important. Even a phenomenon as large as the Mississippian valley forest - all two thousand miles of it - could be relegated by one side to the status of a 'discrepancy'. This is a measure of the distance between Gleason's and Nichols's respective commitments as to what the methodology of the discipline of ecology ought to be - Gleason seeking an ecology based on floristic practice and the individualistic concept, Nichols seeking a more autonomous form of practice, based on the community-unit theory.

Nichols ended by describing various methods of ecological classification, by re-emphasising the importance of classification within ecological practice and by re-iterating that the "importance of the association-type as an ecological unit of classification is generally recognized."[336]

Gleason responded to Nichols's critique by stressing his own claim to be regarded as an ecologist. The debate was partly about credibility. Gleason emphasised the points at which his view and Nichols's coincided. In response to Nichols's attempts to bar him from the ecological community, he made out a case for his being included as a fully accredited member of the profession:-

> "To the uninitiated, it might seem that Dr. Nichols and I are fundamentally opposed. Such is by no means the case. Both of us agree absolutely on the existence of those well-known units of vegetation, the plant associations; both of us agree on the importance of a clear understanding of their nature, of the fundamental causes which bring them into being; both of us are sincerely interested in advancing and clarifying ecological knowledge, a science to which both of us have given much of our time and ability for many years."[337]

Gleason took explicit exception to only one feature of Nichols's discussion of his views - the prominence Nichols had given to the taxonomic analogy. Gleason argued that:-

> "An association is not a species of vegetation. Nay more, the differences between them are so fundamental that even the word analogous can not be used with entire correctness. I readily admit that there are similarities between the two concepts as they exist in the human mind, particularly when we select the concept of the association as held by Dr. Nichols, but that is as far as the similarity extends. Under any concept, a species is a group of individuals the members of which are theoretically related by genesis, and capable of classification genetically when our knowledge is sufficient. But an association has no powers of reproduction. It is merely continued by the reproduction of individual component plants."[338]

Gleason cleverly defused Nichols's appeal to the practice of taxonomy in defence of the practice of ecology by admitting that the former was indeed in a far from desirable condition:-

> " ... every botanist knows the present chaotic state of opinion on the species question, and no ecological principles, especially none so sound as Dr. Nichols', should be supported on so weak a crutch."[339]

[As it happened, Gleason also had strong and somewhat unorthodox views on the question of the species concept - views which were to attract strong criticism from his fellow taxonomists.][340]

The bulk of Gleason's reply to Nichols was given over to a reiteration, in somewhat different terms, of the argument of his recently published paper. He admitted that in many cases, distinctive types of vegetation could be discerned. In this sense, associations existed. But they were produced only under quite specific circumstances:-

> "Now it is well known that it frequently happens that a uniform environment does have a considerable extent and is repeated in other areas. Wherever this happens, a definite plant association develops and is repeated in neighboring habitats. If this condition was universal, neither my paper nor Dr. Nichols' criticism would have been written. But there are other places it does not occur. There the environment changes so gradually from one place to another that the association-concept in Dr. Nichols' sense is no longer applicable."[341]

Gleason concluded by giving perhaps the most concise statement of his own opinion as to the nature of vegetation:-

> "Vegetation then, varying as it does in both time and space, partly through areal variation of chronological change or seasonal or periodic fluctuation in the environment, partly through changes in the flora which by its migration provides the component plants, is a wonderfully unstable thing ... "[342]

In his autobiography, Gleason recorded his impressions of the Ithaca meeting and its repercussions:-

> "That morning the room for the Ecology Section was packed full. Every ecologist was there and practically all the taxonomists as well, because they knew it was one of their own number who was to be flung to the lions. So George made his speech and I made my rebuttal and every ecologist there knew that I was dead wrong. On the way out of the building an hour or so later, Briquet, the taxonomist from Switzerland, walked over to me and said "You are exactly right and all the taxonomists know it."
>
> Taxonomists are not ecologists, however, and for the next several years I and my theories were anathema to all the ecologists."[343]

We have now seen many examples of how Gleason straddled an important professional divide. His perspective on ecological matters was a floristic one - at a time when ecologists wished to be independent of taxonomy. It is, therefore, not surprising that his individualistic concept was regarded more favourably by taxonomists than by ecologists - particularly since Gleason was in the mid nineteen-twenties increasingly devoting the major part of his research effort to taxonomy - and was correspondingly becoming less active in ecology.

Departure from ecology

There is no doubt that Gleason exaggerated the extent to which he was personally an "anathema to all the ecologists". In later years, he often recollected that ecologists came to regard him as "a good man gone wrong".[344] This cannot be taken altogether at face value. On the one hand, it is clear that there was a considerable controversy surrounding Gleason's ideas in the late nineteen-twenties - not all of which is fully represented in print. Ivan Johnston, a taxonomist at the Gray Herbarium in Harvard, wrote to Gleason in 1929:-

> "I have just realised how full of iniquity you are. When your writings can offend a good New England conscience and remove a subscriber from the roll of Ecology, it seems to me that it is time for reformation."[345]

George Nichols encouraged certain of his graduate students to read Gleason's papers, but when one such student [Frank Egler] ventured to find some worth in Gleason's work, Nichols responded:-

> "You wouldn't want other people to think of you as we think of Gleason, would you?"[346]

On the other hand, there is much evidence that Gleason was not so much expelled from the ecological community as gradually came to abandon active involvement in ecology as a consequence of his increasing commitment to taxonomic work and the demands imposed upon a senior member of staff of an institution predominantly devoted to taxonomy. He was, for instance, able to continue publishing ecological papers, despite the controversy he had engendered. Ecology carried his long and detailed discussion of the succession concept in 1927 - this paper emphasised the variability of vegetation in time as well as in space and clarified and amplified the consequences of the individualistic concept for the theory of succession.[347] A fourth quantitative paper appeared in 1929, and an article on the theory of synusiae and the environmental control exercised by one plant upon another was published as late as 1936.[348] He does not seem to have had much difficulty getting his ecological material published. One might expect that he would have experienced such difficulty if he had come to be regarded as being beyond the ecological pale altogether. But it is clear that he remained well respected. In 1929, he was invited by Tansley, the dean of British ecology, to present a paper on the classification of vegetation at the International Botanical Congress to be held in Cambridge the following year.[349] Furthermore, he reviewed Fuller and Conard's English translation of Braun-Blanquet's <u>Plant Sociology</u> for <u>Ecology</u> in 1933.[350] And in 1930, when the journal <u>Ecological Monographs</u> was founded, Gleason was on the editorial board.

Also he did receive some support, in private if not, as far as I am aware, in print, from a number of European ecologists. Gleason met and talked with many eminent European workers during the International Phytogeographical Excursion to Czecho-Slovakia in 1928. He discovered that the Finnish ecologist Alwar Palmgren was basically of the same mind as himself on the nature of the plant association.[351] He also received some support from the Montpelier phytosociologist Pavillard and the Swede Hugo Oswald.[352] However, their support stopped some distance from compete agreement.[353] Gleason also received messages of approval from the eccentric French botanist Felix Lenoble.[354]

That his views attracted more support from Europeans than Americans is not surprising given that, as I outlined in the previous chapter, there was much more of a symbiotic relationship between taxonomy and ecology in Europe than there was on the other side of the Atlantic. However it must be stressed that although he did receive a certain amount of support from European botanists, his views were, even in Europe, taken seriously only by a minority:-

> "I well remember walking through a little patch of steppe with him [Palmgren], a little field of waving Stippa pennata, and finding that he fully accepted the ideas which I had presented in my "Individualistic Concept", and his remark about them "Jetzt ist die Zeit zu sähen". Unfortunately it was not the time to sow; not one person in that party of forty except Palmgren believed, and not one of them would discuss the matter

with me. They were too polite to disagree with a colleague from so far away, and they were genial and friendly conversationalists on all other matters, but on the philosophy of the association, - No!"[355]

The floristic perspective of the European phytosociologists had led to vegetation-units conceived of in floristic terms, not to the abandonment of the vegetation-unit concept, as in Gleason's case.

Gleason was evidently disappointed that his duties at the New York Botanical Garden allowed so little time for ecological research. He was also dissatisfied with the salary he was receiving. He sought to improve matters by appealing, in 1928, to Marshall Howe, then Acting Director of the Garden:-

"It is ten years ago today that I first reported for duty at the New York Botanical Garden. Since that time many improvements have been made at the Garden and I can also detect numerous indications of my own progress. I believe I am safe in saying that my ability to do research work of high quality is second to none in the institution, and that the results of such work as evidenced by printed publication compare favourably with any other's, either in amount or quality. It is certain that my work in taxonomy is accepted with confidence by other systematists both in this country and abroad, who believe that my methods of work lead to reliable results. It is also certain that my work in ecology has attracted more favourable comment and more serious attention from European workers than that of any other American for more than a decade. With the one exception of my work in Puerto Rico in 1926, all of my ecological research has had to be done during vacation time and at my own expense. Until six months ago, all of my work was done without the help of an assistant.

Because of these existing conditions, I place before you the three requests below ...

1. That my salary be placed on a par with that of other men of equal ability ...

2. That it be made part of my regular duties to devote as much as three months of each year to ecological research, provided first, that this time include both the accumulation of data in the field or laboratory and the preparation of the data for publication, and provided second, that unused parts of such time be allowed to cumulate into succeeding years so that work in the tropics or at other distant points may profitably be undertaken.

3. That two hundred and fifty dollars be annually

> appropriated in support of such ecological work to be used for travelling expenses, materials ... "[356]

I have been unable to find Howe's reply in the archives of the New York Botanical Garden. However, it is reasonable to assume that it must have been unfavourable since later that year Gleason wrote Charles Hottes, at the University of Illinois, inquiring as to the possibilities of a return to university life.[357] In April 1929, Hottes recommended Gleason to the Dean for a full professorship in plant ecology.[358] But the salary offered was not an improvement on what Gleason was already receiving at the Garden. Gleason, ever canny on money matters, did not go back to Illinois but he continued his quest for a university job:-

> "By 1929 I had been working several years without an increase in salary and I thought that my increased ability deserved a higher pay. Just then I received hints that I might be welcome as head of the department of botany at the University of Cincinnatti. All negotiations by correspondence went smoothly and in the spring I went out to look the place over. The staff seemed favourably disposed toward me, the dean was willing, and when we parted it was understood that I would be recommended to the Board of Trustees for appointment.
>
> Back at the Garden, while waiting for the official notification, I appeared before our Board of Scientific Directors to report on that famous collection of plants from Mount Duida. I closed by saying that I would probably not be at the Garden next year and that I hoped that the Board would make proper provision for continuing the work. Half an hour later I was called back to the meeting and was asked if a generous raise in salary would keep me at the Garden."[359]

Gleason was thus secured for the Garden and for taxonomy. The cutbacks in public and institutional spending occasioned by the Wall Street Crash and the Depression were shortly to make professional mobility very problematic indeed. Gleason remained in New York until the end of his career. But he never got the special concessions he had sought for his ecological work. In the context of the New York Botanical Garden with its strong institutional commitment to taxonomy and the splendid facilities for taxonomic work it offered, it is not surprising that Gleason's active involvement in ecological work fell into abeyance. This is made further understandable by the fact that, bearing at times a heavy burden of administrative duties - he was Acting Director from May 1936 until February 1938 - Gleason often had little time even for taxonomy.[360]

In 1937 Gleason wrote:-

> "I have done nothing in plant ecology for a long period of time and for the past two or three years have accomplished very little in systematic botany."[361]

This was a matter of regret:-

> "My chief disappointment during the past twenty years has been the necessity of giving up almost completely my original interest in ecology ... At New York I am employed primarily because of my work in taxonomy, to which I am apparently better adapted than to ecology, if I can judge from my reputations in the two fields, although I still consider that my most valuable contribution to plant science is in my various papers on ecology."[362]

Conference at Cold Spring Harbor, 1938

Although Gleason had regretfully and somewhat wistfully abandoned ecology, ecologists had not altogether abandoned him. The Garden was a major centre for botanical research. It attracted a steady stream of visitors from all over America. Botanists would come to use its facilities and consult its staff. Gleason thus continued to meet and talk with botanists interested in ecology and in the nature of the plant association.

The most important of the contacts Gleason nurtured in this way was the energetic and eclectic young ecologist, Stanley Adair Cain.[363] Cain had been a student of Fuller and Cowles, but he could never have been described as a typical product of the mainstream of American ecology.[364] He was always concerned with examining the theoretical principles of ecological practice and felt that the discipline should establish itself upon a more universal, less sectarian basis.[365] With this in view, he went to Pikes Peak to talk to Clements and he experimented with the methods of the Sigma School.[366] Cain regularly passed through New York on his way from the University of Tennessee to Cold Spring Harbor Biological Laboratory, where he taught a summer school in plant ecology. In 1936, and again in 1937, he took the opportunity to talk to Gleason about the individualistic hypothesis.[367]

In 1937, Cain, often an academic impresario, persuaded the Cold Spring Harbor Biological Laboratory to allow him to organise a conference. It was to be held in 1938, under the title "Plant and Animal Communities". Cain wrote to Gleason, telling him of the plans:-

> "You will notice that we have suggested that you present a paper on your opinions concerning the association. You may not care to re-enter this field, but we think that you would have a distinct contribution to make to the program as it is now constituted. We would appreciate your frank reaction to the whole program and especially to the section on association concepts. We are not thinking of the "association" alone but of the "association" as the heart of community problems."[368]

Gleason replied immediately:-

> "I am not only greatly interested in your proposed symposium for next summer but I am also highly complimented to see my name among the suggested speakers."[369]

Cain was thus the principal architect of Gleason's return to the ecological stage. He was to present an exposition of Clements's system to the conference.[370] But he had, by 1938, become more sympathetic to Gleason's views:-

> "I may say that I am closer to your "individualistic concept" - perhaps by the close of the Conference I'll be convinced."[371]

Gleason's 1938 conference paper was a concise and carefully argued synthesis of his 1926 paper on the individualistic concept and his 1927 paper on succession.[372] He argued that the environment was continuously variable in space and time. Vegetation likewise exhibited continuous variation. Individual pieces of vegetation might be highly uniform due to the exercise of environmental control by the dominant plant. Environmental control might also lead to the narrow well defined boundaries between adjacent associations. However this uniformity was not absolute. Over long distances or long time spans radical changes in community composition gradually appeared. Likewise there was no exact repetition of the same vegetation from one location to another. There was only approximate repetition:-

> "It must be remembered that we admit the essential uniformity of vegetation within a single community, and

the frequent striking uniformity between adjacent communities. But the fact that these small cumulative differences do exist is basically important in the consideration of the general concept of the plant-association. They indicate that each community, and for that matter each fraction of one, is the product of its own independent causative factors, that each community in what we now choose to call an association-type is independent of every other one, except as a possible source of immigrating species. With no genetic connection, with no dynamic connection, with only superficial or accidental similarity, how can we logically class such a series of communities into a definite association-type? Truly the plant community is an individualistic phenomena."[373]

Clements was not at the Cold Spring Harbor Conference, having declined an invitation to present a paper entitled "The Monoclimax: the association as a complex organism".[374] But in the discussion period following Gleason's paper, the cudgels were taken up on behalf of organicism by Alfred Emerson, a member of the Chicago animal ecology group, who had, as we saw at the end of the previous chapter, used the 'organismic-community concept of modern ecology' as a 'scientific basis for ethics'.[375]

Emerson had also presented a paper to the conference. Entitled "Social Coordination and the Superorganism", it displayed his continuing commitment to organismic modes of thought and his willingness to extend his discussion from the nature of plant and animal communities to the nature of human society:-

"Wheeler states that human society does not possess an ontogenetic cycle except through colonization, which he compares to the swarming of the honey bee. I would be inclined to view "budding" as well as sexual reproduction of the superorganism, as indications of an ontogenetic cycle, although one is less sharp than the other. Both involve degrees of physiological isolation, reorganisation and development. Social insect colonies show a greater degree of isolation than human communities. Because of the integration between communities, human society is as extensive as the species, while insect society extends little beyond the colony. Great cycles in human society are postulated by Spengler who speaks of the rise and fall of civilisation types ... A great many fluctuations in human community populations have been shown to be correlated with exploitation of new resources and also with greater efficiency in social integration."[376]

In response to Gleason's denial of the reality of supra-individual units of vegetation, Emerson argued that the biological integration of units was as real as the individual units themselves. While an individual organism could legitimately be regarded as a population of cells, it was, nevertheless, also a real integrated unit in its own right. The concept of the human race still had meaning despite the fact that human beings varied and each individual was unique. Holistic units combined to produce larger wholes. Thus despite the dependence of vegetation upon the phenomena of the individual plant, one could still speak of the reality of the community-unit.[377]

Social implications

In the previous chapter I pointed out that the debate which surrounded Clements's organicism extended into the realms of political and social policy. I showed how Clements and the Chicago animal ecology group derived a collectivist social programme from their assumptions of the organismic nature of plant and animal communities. Gleason's individualistic concept likewise carried social implications - if only to the extent that its existence in the scientific literature posed a potential threat to the scientific basis from which Clements and his Chicago group derived their holistic ideology. It is understandable, therefore, that Emerson was moved to confront Gleason's individualism.

Any threat posed by Gleason could not be unduly serious for as long as the individualistic concept was espoused only by a very small minority of scientists. However, its potential social implications were displayed through its adoption by one of the arch-opponents of the ecological technocrats, James C. Malin - whose vigorous opposition to the Clementsians I described in the previous chapter.

Malin contrasted Gleason's "down-to-earth realism" which "excluded completely any idea of vegetation as an organism, even in the sense of analogy" with the formalism of Clements and Frederick Jackson Turner.[378] Gleason's individualistic view with its conception of continuous variability in nature was, in the hands of Malin, a powerful antidote to the determinism of the closed-system theorists:-

" ... if Turner had known and accepted for historical purposes Gleason's point of view in ecology of indeterminate process, he would have been obliged to abandon the Listian theory of stages."[379]

To Malin the existence of the individualistic concept showed that it was possible to achieve a non-Clementsian, non-organismic understanding of the ecology of the Great Plains. The individualistic concept implied the possibility of alternatives to the policies of social and agricultural management proposed by the ecological technocrats of the New Deal. By invoking Gleason, these alternatives could be given the full backing of scientific ecology - an ecology which unlike "the outmoded and wholly erroneous" structure of Clementsianism did not deny the "capacity of man to unfold the potentialities of the mind in discovery of new properties of the earth".[380]

Thus Malin employed Gleason's argument as to the nature of vegetation in a social context - drawing support from the individualistic concept of the plant association for his advocacy of an individualistic social order on the plains. Malin utilised Gleason's individualistic concept to draw social conclusions diametrically opposite to those which Clements and the Chicago animal ecology group drew from the organismic analogy.

There is no evidence to suggest that Gleason was involved in this political debate one way or the other. He, as far as I am aware, drew no explicit social implication from his individualistic concept of the plant association. Gleason did, however, once indicate that there was a strong similarity between his views on vegetation and his views on the development of human society:-

" ... vegetational history exhibits a striking parallelism to human history. Thus Europe has witnessed during the last two millenniums the extinction or absorption of the early Iberians, the persistence of the Basques, the arrival and retreat of the Moors and Turks, and an enormous evolution in culture. Furthermore, the underlying causes of vegetational and human history are similar, even though the human species exhibits an exceedingly complex relation to its environment."[381]

It is perhaps worth noting that, for a variety of reasons, it is not altogether surprising to find a man like Gleason on the individualistic side of an individualist/collectivist political dichotomy. Gleason sprang from farming stock. He cherished his connections with farmers and farming - connections he retained throughout his life. His father's farm remained in the family's ownership and Gleason supervised its management by a tenant.[382] At the time of the Wall Street Crash, when the finances of the New York Botanical Garden were very precarious indeed, Gleason bought another farm in Maryland to which he intended to retreat - to make his living as a farmer should his employment at the Garden be terminated or become no longer financially worthwhile.[383] Like many of his background and class, he admired the life of the homesteader and smallholder:-[384]

> "I believe modern economists call such a place a subsistence farm, and usually allude to it in rather disparaging terms. Nevertheless, it gives the farmer a degree of independence far beyond that of any city dweller or even of any farmer who lives by producing and selling cash crops only. It is the sort of independence celebrated by poets in verse and envied by many a wage-earner in town. It is the continuation into the present day of the life of our ancestors two or three hundred years ago ... "[385]

Such a life style produced "that good old American attitude of courage and nerve".[386]

Thus Gleason was a believer in agrarianism of the Jefferson mould - the sturdy, self-sufficient independent yeoman farmer was the bulwark of the American way of life.[387] He coupled this agrarianism with staunch Republicanism - with all that that entailed for the role which the apparatus of federal government should play in the life of the nation.

On a personal level, he believed in the all-importance of individual conscientiousness and financial rectitude.[388] These beliefs led him to be, within limits, egalitarian. He was proud to number people from all walks of life and levels of society among his friends. He was saddened by the existence of hierarchical social distinctions. He wrote thus of some neighbours of his at Cos Cob in Connecticut:-

> "He was in charge of the stock room at the big electric plant down the road. She was an excellent cook and a

> remarkably fine backyard gardener. Both of them impressed us as people worth knowing not for their wealth or station but just for themselves. So we had them up at our house for a meal, and they reciprocated in due time by inviting us down there. Nevertheless we could never become well acquainted with them. Their whole attitude seemed to be that they themselves were just ordinary folk while we were of the upper class. Thea [Mrs. H.A. Gleason] would like to have known her as a superior housewife and homemaker; I would like to have known him as a sober, hard-working useful citizen, but neither of us could bridge that gap between us."[389]

There are many such stories in his autobiography. When Gleason was working at the Kew Herbarium in London he marvelled at the British meek acceptance of traditional class distinctions.[390] He adhered to the view that a man's place in society ought to depend upon his own individual virtues and efforts. Furthermore he was not beyond using the term 'new-dealer' in its pejorative sense.[391] He disliked communism and left-wing agitation.[392]

For all these reasons, therefore, it is not surprising to find Gleason's name invoked by those on the individualistic side of the collectivist/individualist dichotomy of American social thought. Whether or not Gleason would have sanctioned Malin's political employment of his doctrines, his life style was such that he does not seem out of place in the camp of those who opposed the scientific ideologues of the collectivism and centralism of the New Deal.

Reassessment and recognition

The Cold Spring Harbor conference on plant and animal communities attracted wide attention.[393] Gleason's appearance at it certainly revived some interest in his work among ecologists. He received several letters seeking clarification of his views on the association and related concepts. And in 1940, Frank E. Eggleton, Chairman of the Nomenclature Committee of the Ecological Society of America, invited Gleason to become a member of the Committee.[394] Gleason replied:-

> "The fact that I have been out of touch with ecology for so many years will make me of doubtful value on a committee. There is no use having a member put forward ideas which were out of date ten years ago or fail to understand ideas which are now generally accepted.

Your invitation is the fourth of a similar nature which I have received this year ... Under the circumstances I know that I ought to decline to serve on your committee and yet I hate to lose one last chance to be an ecologist. Before saying no finally would it be possible for me to find out what will be expected of me as a member of the committee."[395]

Gleason's desire not to finally relinquish his involvement with ecology eventually won the day. He joined Eggleton's committee and remained on it until December 1947.[396] This work for the committee gave him opportunities to exert his influence against the persistence of Clementsianism. For example, in 1947, Gleason reacted strongly against a glossary of ecological terms composed by Richard Carpenter:-

"As I look through the various notes which I made on the enclosed list of terms, I realize that I must have been in a particularly bad temper. However the temper was inspired by the remarkably Clementsian flavor of the definitions. Clements is a great man and he has done a lot for ecology but he has erred in attempting to crystallize a lot of colloid facts - and it can't be done. He apparently has thought that it could be done by setting up a series of definitions which reminds one of a woman in our vicinity who believes that she can sink the Japanese navy by concentrating her thought."[397]

As well as his committee work Gleason continued to have opportunities to discuss his ideas on the association with visitors to the New York Botanical Garden. In the forties he had long conversations with Frank Egler, who was doing extensive bibliographic research in the Garden's library, just as he had had with Stanley Cain in the thirties.[398] Gleason came to regard both Cain and Egler as converts.[399]

However it was not until the late forties that the individualistic hypothesis received public support in America. In 1947, Cain and Egler both argued that ecologists should conduct a general reassessment of Gleason's theory.[400] And in the late forties, two field studies got under way, in Wisconsin and in Tennessee, by John T. Curtis and Robert H. Whittaker respectively, which were to provide new quantitative evidence for the individualistic hypothesis.[401] Curtis and Whittaker were major advocates for the individualistic concept throughout the fifties. However the individualistic concept was still intensely controversial and the community-unit theory of the plant association retained many adherents. It is perhaps significant that in 1956 when Gleason was presented with the Certificate of Merit of the Botanical Society of America, the citation made no mention whatsoever of his work outside taxonomy.[402] However, by the mid-fifties the tide was certainly running strongly for Gleason. Curtis wrote to Gleason in 1955:-

> "[American phytosociology's] current status seems to be a state of flux with a great majority of the investigators rapidly coming around to the Gleason individualistic hypothesis or a reasonable facsimile thereof. The last major holdout appears to be in the group of range managers in the Plains States who are still imbued with Clementsian doctrine. It is noteworthy, however, that no important papers on vegetation have appeared in the last two or three years which actually used the Clements system. The old ideas seem to die harder in those who talk about ecology rather than those who are actually practising it.
>
> As you have probably gathered, we consider ourselves your disciples. With each passing year, we are more and more impressed with the insight you showed and with the clear manner in which you expressed the interrelations existing in vegetation. It becomes more and more difficult to understand the apparent indifference or actual opposition to your ideas. There must have been a kind of mass hypnotic state among the ecologists."[403]

As is perhaps understandable, given his role as a major protagonist in the renewed debate surrounding Gleason's theories, Curtis over-emphasised the extent to which the opposition had been vanquished and the individualistic concept generally adopted. He also erred in identifying his opponents only within the remnants of Clementsianism. Ecologists who had no great love for Clements - principally students of W.S. Cooper - were yet to return to the barricades on behalf of their own version of the community-unit theory.[404] However, Curtis's remarks show that the process of reassessing the significance of Gleason within the history of the discipline was well underway. Gleason was to be represented as the lost founding father of the discipline - the real precursor of modern ecology.

In 1959 Gleason was honoured by the Eminent Ecologist Award of the Ecological Society of America. The encomium was spoken by Stanley Cain, who was also chairman of the Nominating Committee:-

> "Dr. Gleason was never one to fit into pigeon holes the facts which fell under his acute sight, and I have

> no interest in trying to classify him other than as an "individualistic ecologist" who has bothered a lot of other ecologists with his "individualistic association" concept. He has always been a man of ideas. But these are the ideas arising from what he has observed in nature not ones he has tried to fit nature to. He has neither been impressed nor foiled by the philosophic creations of other ecologists, for he has always tested their ideas concerning the association, succession, the climax, environmental controls, and biogeography against what he knew in nature."[405]

Such acclaim gave Gleason great pleasure.[406] He felt vindicated by this revival of his individualistic concept:-

> " ... I wrote to Curtis of the University of Wisconsin, and asked him how generally ecologists now accepted my theory. Curtis replied that everyone did, with the possible exception of a few die-hards ... Well, it was a long wait, but it gives me great satisfaction in my old age to know that I have made some real contribution to plant ecology."[407]

Gleason was entitled to feel vindicated. The association-unit theory, as it had been employed by Nichols and Cooper, was indeed in retreat - at least in America. But the reason for the fresh adoption of the individualistic hypothesis did not lie entirely in its inherent virtues, considerable as these were. Changes in the social context within which ecology was practised also played a part. Furthermore the individualistic hypothesis adopted by Curtis and Whittaker was subtly different from Gleason's own version. But these developments are another story and merit a full and detailed treatment of their own. They will be studied in the following chapter.

Conclusions

We have now followed the full extent of Gleason's career. We have seen how an early attraction towards the outdoors led to an interest in natural history as a hobby and the study of botany at university. Success in that study led him to aspire to become a professional botanist. The aptitude displayed as an undergraduate, the skills developed in private study, led to him being chosen to receive intensive training in taxonomic botany. But being a student at one of the few American institutions at which ecological research was being done, at a time when influential exemplars in plant ecology were being produced, Gleason began to practise the nascent specialty of ecology. Initially Gleason followed closely the model of Cowles, but gradually developed an approach more distinctively his own. I have argued that this approach was characterised by a commitment to conceiving of the plant association and other ecological phenomena in floristic terms. This is explicable in terms of Gleason's early floristic training. Most ecologists wished to retain the association as a distinctive object of ecological study, defining an autonomous reality. Thus they rejected the individualistic concept. Other ecologists thought also in individualistic terms but approached ecological research from a background in physiology, not taxonomy, so had little common ground with Gleason.

Gleason was one of the most prolific ecologists of the 1900s and 1910s. But he always kept up his interest in floristic botany. Financial consideration and the promise of fewer teaching commitments led him to accept the offer of a job at the New York Botanical Garden. In that institutional setting it was inevitable that his ecological work should take second place to his taxonomy. But he abandoned ecology only gradually, with regret and not without making calculations as to the advisability of returning to ecology and university life. However, personal contacts with young botanists facilitated by his institutional position, enabled him to keep his ecological ideas in currency and eased the way to a revival of the individualistic concept when conditions became favourable.

Thus, we have seen that Gleason's professional activities were determined by skills and commitments gained both within and without his professional training. We have seen the great importance of the fact that he early acquired skills in floristic botany. But equally important in shaping his career and the content of his work were his love of the outdoors and his aptitude for mathematics. One might also mention his commitments to a society based on hard work and individual virtue. Furthermore, I have demonstrated how the reception of Gleason's individualistic hypothesis is explicable in the light of the interests and skills of his fellow ecologists.

The character of Gleason's early ecological work tells us much about the nature of ecological practice in the discipline's formative years. A comparison of the view-points of Shreve and Livingston, Gleason and Cowles, affords much further evidence to support the view that prior training and skills are important in structuring research activity. The competences already possessed by those entering the field of ecology systematically organised each new recruit's approach to the phenomena of vegetation. This was particularly obvious in the early decades of the century - before ecology was fully institutionalised and therefore before recruits to ecology had generally received an undergraduate and graduate training in ecology itself. The constructive orientation of prior competences is evident in early American ecology even despite the wish of many ecologists to make the discipline's subject-matter as distinctive as possible in order to enhance the autonomy of the specialty. Thus Livingston had special training in physiology and, having entered ecology, remained a physiological ecologist. Cowles was originally a student of geology and, on becoming a botanist, founded the physiographic school of ecology whose theory was based on the principles of geomorphology. Gleason's equivalent early competence was in floristic botany and he continued to articulate a floristic perspective on ecological matters, even after he had adopted much of the Cowlesian physiographic paradigm.

We have also seen how Gleason made career decisions in the light of where he considered his personal interests lay, on matters of financial rewards, life-style and the like. I have tried to give a composite picture of how all these skills, commitments, interests and contexts, combined to produce, as it were as a resultant, the shape of Henry Allan Gleason's scientific career and the development of his ideas as to the nature of the plant community.

CHAPTER FOUR

THE INDIVIDUALISTIC HYPOTHESIS REVIVED

Introduction

By the nineteen-twenties, with the work of the Zurich-Montpelier and Uppsala schools in Europe and that of Cowles and Clements in the United States, the community-unit theory had taken on its mature modern form. As we have seen, up until the nineteen-forties, this view of the nature of vegetation was almost universally accepted - although many ecologists quarrelled with Clements over the very high levels of integration within each unit which Clements claimed to discern. Only one ecologist in America (Gleason), and no more than half-a-dozen elsewhere, had publicly disagreed with the assumption that there were natural kinds of vegetation.[1] So fully accepted was this theory, so much was it an unquestioned and implicit framework for practice, that it did not even have a definite name until 1956. It was only then that R.H. Whittaker, an American ecologist and one of the first men to revive the individualistic hypothesis, dubbed it the 'association-' or 'community-unit' theory.[2]

In the late forties and early fifties, this unanimity amongst American ecologists as to the fundamental nature of the units of vegetation began to break down. Explicit expressions of dissent on this matter first appeared in print in 1947 - when a single edition of the leading American journal Ecological Monographs contained three articles, all from prominent figures in the American botanical community, which expressed disagreement with the community-unit theory and support for the individualistic hypothesis.[3] Gleason's individualistic hypothesis, it must be remembered, had been available as a potential resource within the discipline since 1917 and had been re-stated by Gleason in 1926, and again in 1939. But it had received scarcely any public support at all, until these three articles appeared together in 1947.

In the nineteen-fifties, Gleason's individualistic hypothesis was to attract much attention. Major field studies were based upon it.

Much debate was again occasioned by it. By the mid-sixties, the individualistic hypothesis had become, more or less, generally adopted - in preference to the community-unit theory as employed by Clements, Nichols and Cooper.[4] In this chapter I shall examine why Gleason's theory was re-assessed in the late forties and early fifties. It is not my intention here to go into any great detail as to the nature of the technical arguments or empirical evidence put forward by the new champions of the individualistic hypothesis. Nor will I be concerned with documenting the wider adoption of the individualistic hypothesis. Such matters will be mentioned only briefly. My principal concern will be the social and institutional background to this transformation - for I believe that it was the actors' perception of adverse social circumstances which led to the production of new technical arguments and new empirical data and to the re-interpretation of theory.

Clements's work had, of course, been criticised in print many times before 1947, not only by those who found his views on systematics and speciation unacceptable, but also by his fellow ecologists.[5] Clements had what is a strange position in the history of biology in being the acknowledged leader of a field to which he was always marginal. He was always marginal in the sense that the Clementsian doctrine was never generally accepted in its entirety. He was the most creative and productive ecologist of his generation, but much of his theorising was always regarded by his colleagues as being fanciful and overblown. Perhaps an American ecologist asked in the nineteen-thirties to name the greatest American ecologist would have responded in the manner of the Parisian critic who, when asked to name the greatest living French novelist, was forced to reply, "Victor Hugo. Hélas!"[6]

As we have seen in the previous chapter, several aspects of Clements's work had been subjected to criticism by Cooper and by Nichols, to name only two. But these criticisms had not extended, save in the work of Gleason, to expressions of doubt as to the existence of community-units.

New criticisms

In 1934, R.F. Griggs described the difficulties he had in applying the community-unit theory to the vegetation of the Arctic:-

> "In the temperate zone vegetation is rather clearly segregated into more or less well-marked associations, like beech forests, oak forests, pine woods, swamps and bogs ... when one goes to the arctic he naturally expects to find similar plant associations, but instead he meets a bewildering mixture of plants of all sorts jumbled together in seeming defiance of the principles of plant association learned in low latitudes."[7]

Griggs's conclusions were not however the same as those at which Gleason had arrived, when confronted with similar problems in the tropical forest. Griggs argued not for the general inappropriateness of the community-unit concept but rather that its present inapplicability to boreal vegetation was evidence that recovery from the effects of general glaciation in the Ice-Ages was not yet complete. Arctic vegetation was still in a "process of active readjustment".[8]

However, in 1941, Hugh Raup, an ecologist and plant geographer at Harvard, used Griggs's work to emphasise the hypothetical nature of the notions of equilibrium, climax and succession as then conventionally employed.[9] He argued, in effect, that the theory of large-scale occurrence of climax vegetation-types determined uniquely by overall climatic conditions was perhaps false. This implied that much previous work on the determination of successional changes had been predicated upon a false premise.

In 1942, Raup returned to the argument to voice a more general criticism of Clementsian methodology:-

> "Ecological geographers, starting with the assumption of a causal relation between plant and environment, have built the entire structure of their science upon efforts to prove its significance and to interpret the distribution of plants on the basis of it. The initial reasoning, therefore, has not been by simple induction from a body of empirically and naively determined facts, but from a system of working hypotheses based upon assumptions of mutual cause and effect ... In his earlier work on Research Methods in Plant Ecology (1905) Clements states clearly that his premises were in environmental determinism. In the latest textbook of Weaver and Clements (1929, 1938), however, the causal relation is obviously no longer an assumption but an established fact, and no apology for it is given."[10]

Raup argued that the Clementsian system was not only erroneous in detail but was fundamentally misguided. It was overly deductive and hypothetical. Raup, however, criticised not only the Clementsians but the prevailing ecological orthodoxy quite generally. Like James Malin, he argued that disturbance was quite universal even within virgin vegetation. He argued that long-term stability was never achieved and that a high degree of supra-individual integration did not exist within the plant cover. He emphasised the importance of accidental and catastrophic events such as hurricanes.[11] Like Gleason, Raup brought to his ecology considerable experience in floristic botany - he had been an assistant in the Arnold Arboretum.[12] And, like Gleason, he emphasised the importance of floristic plant geography and the study of the individual plant species rather than assemblages per se. He broadly supported Gleason's critique of the organismic metaphor and the community-unit theory.[13] However, in the early forties, Raup did not explicitly deny the existence of natural kinds of vegetation.

Thus, in the early nineteen-forties, the following situation obtained. Most ecologists, like Cooper and Nichols, distanced themselves from the totality of the Clementsian system. But they routinely worked with the notion that vegetation existed in natural units. On the other hand, Gleason, explicitly, and Raup, implicitly, denied the reality of definite units of vegetation. Both these critics took issue not only with Clements but also with mainstream opinion at many crucial points. Gleason, however, was no longer a practising ecologist. Raup was on his own.

In 1947 a new note was struck. In that year, Herbert Mason, Stanley Cain and Frank Egler all cast doubt upon the objective reality of the plant associations described by American ecologists and explicitly criticised the community-unit hypothesis. These publications taken together constitute an event of great significance in the history of plant ecology.

I shall look at each of these papers in turn and consider in detail the criticisms that each author raised against the community-unit theory. A pattern of common emphases will emerge. It will be seen that not only did Mason, Cain and Egler agree on the deficiencies of the community-unit theory, they shared a pessimistic appraisal of the condition of the discipline of ecology as a whole. I shall argue that it was no coincidence that these two forms of dissatisfaction occurred together. By criticising the community-unit theory, Mason, Cain and Egler were advocating a change in the overall strategy of the discipline.

A background of problems

But first, in an effort to illuminate the background to Mason's, Cain's and Egler's criticisms, I will consider the situation of ecology as a scientific discipline in the years leading up to 1947. It is here that the key to an understanding of their advocacy of new directions for the discipline lies.

American ecology in the nineteen-forties was in a lowly position. It lacked prestige and prominence within the scientific community and it was suffering thereby. It had been under pressure for some time as to its legitimacy as a scientific discipline. Veterans of the thirties and forties recalled that the specialty's pretensions to scientific status were the subject of much sceptical comment.[14] A fine illustration of the pressures the field disciplines found themselves under is provided by Henry Allan Gleason's experiences as Director of the University of Michigan's Biological Station.[15]

Gleason was appointed Director of the Station at a time when its very existence was being cast in doubt by the criticisms of influential persons within the university. His predecessor as Director had been the founder of the Station, Jacob Reighard, the Professor of Zoology. Gleason saw tactical disadvantages in the regime of the summer school as instigated by Reighard:-

> "Jacob Reighard ... was a great outdoor man. He liked fishing and hunting; he liked his cottage in the woods of the Upper Peninsula. As a result of his own likes, he thought that all students of nature, both botany and zoology, should also be completely at home in the woods, should like the wilderness and be on familiar terms with all the plants and animals. In other words, a botanist or a zoologist should be a sort of Boy Scout on a more elevated plane."[16]

Reighard had required that all students enrolled in the summer school undertake a weekend camping trip, which involved no scientific work but during which the students learned to pitch their own tents and cook their own meals. Gleason saw that this sort of activity was regarded as frivolous by members of the faculty not involved with the Station. More importantly, it lessened the esteem in which the Biological Station was held by its paymasters:-

> "The requirement was printed in the annual announcement of the Station and had been at least one of the causes why the University Administration regarded the Station as a camping party."[17]

Gleason worked hard to increase the student enrolment of the summer school and to convince faculty and administration of the need for field-work within the teaching of biology and of the legitimacy of field research. As one of his first acts as Director, he abolished the camping trip. Eventually he had to face an inspection from Kraus, the Dean:-

> "We showed him everything that was going on, took him on brief excursions, let him see a class or two at work, showed him the research that we were doing. I shall never forget his last afternoon, when he and I sat in my tent and discussed Station affairs. I had convinced him that we were really doing scientific work and not merely camping out, that the students were learning ... that there actually was opportunity for research. The Dean told me all his misgivings and told me of the opposition to the Station held by some of the professors ... but in the end he promised his full support for 1914. The Biological Station was saved ... if I had not convinced Kraus of the quality of our work, and Kraus really had to be convinced, the Station would have been closed forever at the end of the 1913 session."[18]

Under Gleason's directorship, the Station gained its first permanent building, the Haughton Laboratory. With student enrolment up and an increased financial appropriation, its continued existence was assured.

The trouble Gleason experienced over the funding of the Station well illustrates, on a small scale, the institutional stresses which the new specialty of ecology was suffering. For ecology, although conceived in the enthusiasm for the New Botany, always stood a little uneasily with the other subjects nurtured by that enthusiasm. It was a field subject, devoid of much of the paraphernalia of laboratory science. It was more often observational than experimental.

Other scientists did not always appreciate how ecology was different from high school natural history, or worse, weekend backwoodsmanship - pastimes rather than scientific professions. Therefore ecology was exposed to accusations of lack of scientific rigour and intellectual seriousness. In 1944, J.D. Covington complained to the Ecological Society of America:-

> "Ecology is commonly omitted in the introductory course in biology or zoology, due to either of two mistaken concepts; ecology is either grammar-school natural history and hence unworthy of the college freshman level or it is too advanced and difficult. Neither view is correct."[19]

Eugene Odum encountered similar problems:-

> "When I first came to the University of Georgia as a young instructor in 1940, my suggestion that a course in ecology be included in a core curriculum for majors received an exceedingly cold reception. My colleagues of those days confused ecology with natural history and voiced the opinion that no new ideas or principles were likely to be revealed in an ecology course that had not already been covered in courses in taxonomy, evolution, physiology and other subjects considered more basic."[20]

Ecologists, wishing to escape from the unpleasant consequences of being so perceived, were faced with the task of persuading their scientific peers and paymasters that they were doing real science.

Such problems had long dogged the discipline. We have already seen, in Chapter Two, how Clements sought to increase ecology's prestige by adopting the methodology and vocabulary of the indubitably scientific discipline of physiology. The problems of dubious status, which called forth this strategy of Clements, may be regarded as a continuing part of the collective experience of members of the specialty. As we shall see, the subject's low status was a source of embarrassment and, more importantly, frequently a cause of financial stricture. I will argue that the need to resolve these difficulties exercised a formative influence upon the character of the specialty as a whole.

Ecology in the late forties was not even as relatively prosperous as it had been in the late thirties when ecologists and applied ecologists had benefited from the increased interest in land management and conservation associated with the New Deal.[21] After the

Second World War, and particularly with the new Republican administration, this was no longer the growth area it had been.[22] Job opportunities were few even for the better students; advancement opportunities for established ecologists just as scarce. Few studentships or fellowships were available. Here again, the comparison with other disciplines was painful:-

> "Although large sums of money are being made available through scholarships and research fellowships for capable young students interested in doing research in numerous scientific fields, only very limited amounts of money are available for students interested in the botanical field and especially ecological research."[23]

The discipline was still under adverse scrutiny. In 1948, D.B. Lawrence, the editor of Ecology complained of:-

> " ... the people who critically evaluate ecological research and constantly question the right of ecology to be considered a science."[24]

Symptomatic of these troubles, the membership of the Ecological Society of America had not grown since 1920 - after an initial period of expansion immediately following its foundation in 1914.[25]

Ecology was suffering, for instance, through not being seen to be associated with fields of the brightest theoretical promise. The University of Chicago's leading ecologist, H.C. Cowles, a very distinguished scientist, retired in 1934.[26] Although he was replaced, plant ecology lost something of the status it had previously enjoyed in that institution. The University of Chicago was a major recipient of money from the Rockefeller Foundation which in 1933 redirected its funds from nuclear physics into biology - specifically into the areas of biochemistry and genetics.[27] This was the era when physicists first began to become molecular biologists.[28] Ecology lost out - it did not benefit from this new influx of funding or personnel into biology.

A similar change of direction was made by the Carnegie Institution, which had been a generous source of funds for ecological research, virtually from the very beginnings of the subject in America.[29] In the 1900s and 1910s, Shreve, Cowles, McDougal, Cannon, Livingston, and Spalding all received financial support from the Carnegie. The Desert Laboratory was founded with Carnegie funds in 1903, and remained an important venue for research in ecology and ecological physiology for forty years. Clements joined the Carnegie in 1917, working first principally at the Desert Laboratory. In 1917 the Carnegie also took over the Alpine Laboratory at Pikes Peak, Colorado, which had been established by Clements and his fellow members of the Botanical Seminar of the University of Nebraska. A third laboratory, the Coastal, was founded at Mission Canyon near Santa Barbara, in 1925. Clements had, by this time, become head of a specially created section for ecological research within the Carnegie Institution. To the Carnegie, therefore, is due a considerable part of the credit for the successful institutionalisation of ecology in America in the early twentieth century.

By the late twenties, the Carnegie had lost the first flush of its enthusiasm for ecology. In 1927 the Ecology section lost its independence and became part of the Division of Plant Biology. Clements lost several research assistants in the re-shuffle. He lost considerable status in the process. Neither he nor ecology ever recovered their former position within the Institution - although he continued to be supported by Carnegie funds until his retirement in 1941. The Carnegie Institution, like the Rockefeller Foundation, was intent on redirecting its funding toward other, more promising, areas of scientific research. This was particularly threatening for Clements. He evidently felt that his work was misunderstood and his personal worth unappreciated by the executives of the Carnegie.[30]

One of the problems was that Clements, like many other early ecologists, was a Neo-Lamarckian.[31] He held that the form of the plant was the product of the direct action of the environment. Natural selection could not operate upon adaptive forms since they were completely at harmony (epharmonic) with the environment which had produced them. Mature plants were seldom 'unfit' in the Darwinian sense. Clements sought therefore to alter plant form, and indeed transmute species, by transplant experiment. By the late twenties he believed that he had succeeded in converting "several Linnean species into each other".[32]

The Carnegie had also begun to fund the work of Clausen and his associates at Stanford.[33] These researchers were convinced that the environment selected particular genetic strains rather than directly influencing changes in the form of the plants. Clausen argued, in direct contradiction to Clements, that environmental modification of the phenotype was of relatively minor importance and not heritable. This was the view which became part of the prevailing orthodoxy in evolutionary biology. In the face of the Stanford results, Clements's continued assertion of his Neo-Lamarckian claims served only to discredit him - respectable as such claims might have been twenty or thirty years earlier.

By the time of his death in 1945, Clements, the major theoretician of the pre-war years, was no longer a figure it was useful for young ecologists to identify with closely if they wished to be regarded as within the mainstream of biological research. Stanley Cain, for instance, in the preface to his 1944 book The Foundations of Plant Geography acknowledged the benefits he had received from his conversations with Clements, but was careful to distance himself from Clements's view on speciation:-

> "To F.E. Clements, I wish to express appreciation for his hospitality at the Alpine Laboratory and for many hours of his inspiring conversation. Anyone familiar with his Neo-Lamarckian concepts will realise the extent to which I disagree, yet I wish it known that I consider him a great ecologist of profound learning."[34]

This was the era of the New Darwinian synthesis.[35] By making the most modern genetics and quantitative population studies compatible with, and apparently reinforced by, the achievements of traditional descriptive disciplines such as palaeontology, morphology and embryology, the Neo-Darwinians had constructed a theory of impressive scope and power, which had more or less silenced (if only briefly) the debate over the mechanism of evolutionary change. The New Synthesis had become the most prestigious theory in the biology of the day. It seemed to draw support from the whole of biology and to have implications for every sub-discipline. The New Synthesis seemed to emphasise the unity and enhance the scientific status of the science of biology. As Provine has written, "By 1940, any evolutionist not a neo-Darwinian was clearly out of step with the times".[36] Adherence to the New Darwinian Synthesis was held to be part of a biologist's scientific credentials and a mark of his serious commitment to his subject. But Clements was out of step. Continued support for Clementsian views amongst ecologists was not liable to impress geneticists or even taxonomists, and was not likely to aid their acceptance as full members of the community of biological scientists.

The distance between ecology and the New Synthesis meant that unflattering comparisons could be made between the state of ecology and other more apparently progressive botanical specialties - specialties with which, in some cases, ecology had long sustained a rivalry. Raup was pleased to point this out:-

> "The main point to be made here is that floristic geography has been enormously enriched by genetic views in the study of populations, and by the contributions of genetics and cytology to the problems of taxonomy. These views are remarkably free from environmental determinism, and the reasoning is rigorously inductive, without pretense of a direct attack upon the ultimate complex causal relationships. Physiological plant geography, on the other hand, has been rather resistant to the inroads of genetical ideas, perhaps owing to its inherent preoccupation with the external environment of plants. One of its basic ideas has always been a causal sequence in which the habitat comes first, but the field of floristics now comes forward, aided and abetted by students of genetics, with the idea that the plant itself, by its inherited existence, contains causal elements which cannot be readily subordinated to the external environment."[37]

If, in every other field, Clements's views were regarded as antediluvian, it is not to be expected that a peripheral and insecure specialty eager for recognition, such as plant ecology in the forties, would long sustain any allegiance to him. Given the general situation, it is not surprising that the younger American ecologists should seek new directions for the discipline to carry it out of a state of low prestige and low funding.

Some other circumstances eased the way for change within the discipline. Clements had died leaving behind few active students. He had spent the last thirty years of his life working not in a university, but at the Carnegie Institution. There had been other important changes in the discipline's personnel. The retiral of Henry Cowles has already been mentioned. George Nichols, another major figure among pre-war ecologists, had died in 1942, while still active in research and teaching.[38] Nichols had been Eaton Professor of Botany at Yale and although he had interests in other fields of botany (in particular mycology), he may fairly be regarded, with Cowles, as one of very few American ecologists to have achieved an elevated position in an academic institution before the Second World War. American ecology between the wars was dominated by four men - Cowles, Clements, Nichols and W.S. Cooper of the University of Minnesota. After 1946, only Cooper remained. The demise of Nichols is particularly important in the present context - that of the revival of the individualistic hypothesis - since he had been, in the twenties and thirties, one of the most determined opponents of the Gleasonian view of vegetation. Theoretical changes were correlated with and facilitated by these changes in personnel.

A move away from old forms of theory may be understood as part of a general strategy aimed at rendering the discipline of ecology more similar to those parts of biology which at the time were centres of greater scientific prestige and recipients of more generous funding, such as physiology, genetics and those disciplines of general biology, embryology for example, which were associated with the new evolutionary synthesis. We shall see this change being advocated by Mason, Cain and Egler.

Here as at many points in the history of American ecology, the importance of Clementsianism should not be over-estimated. Relatively few of these authors' critical remarks were addressed directly toward Clementsian tenets _per se_. Mason, Cain and Egler criticised the state of ecological orthodoxy as a whole. However, such criticisms of Clementsian doctrine that they did make were significant. Clements had been, despite everything, a giant amongst ecologists. And, perhaps because of his relative isolation within the discipline and certainly because of the extreme character of his methodological prescriptions, Clements's style of ecology stood as a potent symbol of the ecology that was now old-fashioned. Clements's ecology, represented as subjective, descriptive, deductive and speculative, provided a most vivid and convenient image of what the new ecology could not afford to be.

Herbert Mason's criticisms

Mason's article was a revised version of a paper given to a conference on plant geography organised jointly by the Ecological Society of America and the Association of American Geographers. The conference took place in Boston in 1946. The date is significant because of the hiatus occasioned to much ecological activity by the Second World War. Considerable numbers of the younger members of the profession had been dispersed from their home bases by becoming involved, one way or another, in the war effort. Others had their entry into academic careers or graduate training delayed by the war. So as civilian activity gradually returned to normal in 1946 and 1947, there were re-adjustments to be made. Furthermore, the institutional circumstances of American science were somewhat altered by the Second World War. As a result of the role science had played in the war effort, public funding for science was more readily available than it had been before.[39] But much to the distress of the Ecological Society of America, the public paymasters were not looking in ecology's direction.[40] Compounding its lack of prestige among its scientific peers, ecology lacked an obvious role in the national effort - this being important at a time when, and in a country in which, the ideology of a national science was taken seriously.[41] It was time for a change.

Mason was not a professional ecologist. The fact that Ecological Monographs was publishing the proceedings of a conference organised only partly by the Ecological Society explains the presence of a paper by Mason in an ecological journal. His main interests lay in study of the evolution and distribution of flora. He had trained as a taxonomist. He was Director of the Herbarium of the Department of Botany at the University of California, Berkeley - a department notorious at the time, and for some time afterward, for its lack of support for ecological research.[42] Mason was well-known as an outspoken critic of what he saw as the scientific pretensions and shortcomings of ecology - opinions which were also voiced by several of his colleagues and students.[43]

Mason would never have called himself an ecologist - but the subject-matter of his research was interrelated with that of vegetation science and his work did have ecological implications. He pointed these out forcibly in his 1946 paper which was a forceful advocation of the general applicability of the new Darwinian synthesis to both floristics and vegetation science. Mason argued that floras and plant communities were best thought of as assemblages of inter-breeding populations - a perspective explicitly derived from population genetics. There were, therefore, no integrative processes working above the level of the population:-

> "The organic functions of the population, then, are solely the functions of population genetics and result from reproductive and genetic activity within the population ... Furthermore, there are no organic functions that operate between genetically unrelated populations ... A community made up of such populations has neither organic nor functional unity but is an aggregation of independently operating populations of interbreeding individuals. Each such population functions strictly on its own behalf without consideration of any unrelated associated population."[44]

Therefore Mason concluded:-

> " ... that floristic evolution is activated by the interplay between environmental conditions and genetic and physiological phenomena that induce migration, bring about extinction, and select those genetic races within the species population that are preadapted to the new conditions. The production and selection of the genetic races must be construed as steps in the evolutionary process known as natural selection."[45]

'Natural Selection' was a key term - as were 'genetic' and 'physiological'. The last two recurred in nearly every paragraph of the paper. Throughout its entire length, Mason demanded that both floristics and ecology "lean heavily upon the logic of ... physiological interpretations".[46] The principal implication of Mason's argument was that ecology must become similar in explanatory structure to the most prestigious areas of contemporary biology. It must become Darwinian. It must base itself on the models of genetics and physiology. Genetics was attractive to Mason as an important component of the Darwinian synthesis and an increasingly successful discipline. Physiology was, as we have seen in the previous chapters, the perennial exemplar of a 'hard' experimental biological science.

It was essential, according to Mason, if ecology was to be made harmonious with these prestigious disciplines, that the community-unit theory be abandoned:-

> " ... such dynamics [i.e. the physiology of the individual and the genetics of the population] leave little room for concepts of vegetation in time or space that regard the community as a functioning unit made up of wholly interdependent individuals. The interdependencies within the community are strictly within the sphere of parasitism and symbiosis and as such are the special problems of special cases."[47]

The community-unit theory, as articulated by Clements and others, necessitated the assumption that integrative processes worked at the level of the community. Otherwise the organismic analogy, or arguments about the whole being greater than the sum of its parts, had no meaning. Mason argued that such an assumption was incompatible with the Neo-Darwinian emphasis upon explanation in terms of individual organisms. Individuals, possessing differing competitive abilities, differed in the number of offspring they produced - thus altering the gene ratios of succeeding generations.[48] All large-scale biotic change was taken to be the product of these differences between individuals and the resulting alterations of population gene ratios:-

> "Floristic history, because of the lack of reality of precise associations through time and because of the lack of functional unity of the plant community, becomes the history of an aggregation of independently operating dynamic systems, each of which is meeting its problems in its own way."[49]

Conveniently for Mason, the abandonment of the community-unit theory which he advocated did not necessarily entail the leaving of a complete vacuum in ecological theory - there already existed a rival theory which could be called upon to take its place:-

> "We may agree with Gleason [1926] as to the coincidental nature of the plant community ... The plant community, then, possesses only coincidental unity based upon simultaneous environmental tolerances for the overall environmental factors."[50]

The Gleasonian concept of the plant community had the great virtue, for Mason, that he could present it as being consistent with the individual and population emphases of Neo-Darwinian inquiry. As Mason expressed it, the individualistic concept could be regarded as harmonious with a physiological and genecological interpretation of the phenomena of vegetation. Gleason's emphasis on explanation at the level of individual plants seemed to allow the possibility of rapprochement between vegetation science and the Neo-Darwinian research programme.

It is important to note that compatibility with Neo-Darwinism should not be regarded as an inherent or essential feature of the individualistic hypothesis. There is certainly no evidence that Gleason so conceived it. Nowhere in his expositions of the individualistic hypothesis did Gleason connect it with Darwinian theory. Gleason did not employ the term 'Natural Selection' nor any other of Mason's key words in expositions of his views on the plant association. Certain other botanists have chosen to regard Gleason's work in quite the opposite light - as anti-Darwinian in implication.[51] Gleason's insistence that species were distributed at random and by chance seemed to deny the possibility of the structuring of the plant community by micro-environmental selection and competitive advantage.[52] The premises of Gleason's statistical approach could be regarded as involving a denial of the fundamental Darwinian tenet that each species grew where it was best adapted to grow. Mason therefore had interpretative, or at the very least selective, work to do before he could present the Gleasonian individualistic concept as compatible with Neo-Darwinism. This was not obviously or necessarily the case.

Gleason's work could have been interpreted in several different ways - a Darwinian Gleason merely being one of them. It was the high standing of the Darwinian approach in biological science generally which led to Mason expressing Gleason's ideas in Darwinian terms. In the forties, biological theories were being judged by yardsticks different from those which had applied when the individualistic hypothesis was first proposed. Mason's version of the individualistic hypothesis was altered in response to these new circumstances.

Stanley Cain's criticisms

In the previous chapter we saw that, in the late nineteen-thirties, Cain had much personal contact with Gleason and learned of the individualistic hypothesis directly from its originator. Eventually Cain had declared himself to be convinced. It is not surprising therefore to find Cain, now Professor of Botany at the University of Tennessee, among those who were the first to call publicly for a re-assessment of Gleason's case.

Stanley Cain's 1947 paper, also given at the 1946 conference in Boston, was not quite so combative as Mason's. Cain did not so much attack the alleged unscientific basis of contemporary ecology, as worry over it. In describing the methods used to determine vegetation types, Cain wrote:-

> " ...the exercise is an intellectual one of a different order from everyday physics, chemistry and mathematics. I will not say that this type of ecology is an art - but it is something less than an exact science."[53]

And again, later in the paper, referring to contemporary European ecological practice, he maintained:-

> "New investigations of the phytosociologists produce results with the appearance of a high degree of accuracy, with statistical data on coverage, frequency, density, constancy, and fidelity, with impressive tabular comparison of stands of an association. And yet it seems to me having tried these methods myself, and without impugning the honesty of the investigators, that there is more artifice than science in the selection of stands for representation of the association."[54]

However, to Cain, it was not <u>necessarily</u> a bad thing that the intuitive skills of the trained ecologist should have a role to play in understanding the phenomena of plant communities:-

> "Unless one arbitrarily limits his attention to a single factor or a restricted group of factors ... he is confronted with the necessity of a more or less subjective delimitation of natural areas ... the number of operative factors is so great and the mutual effects and interrelations so complex, that the investigator must decide somewhat on the basis of how he feels about the matter just where the boundary of a particular area is to be recognised. This is in the nature of things and not to be decried but it ... gives the cloak of authority only to the scientist with wide experience, broad knowledge and that imponderable which may be called good biological sense."[55]

The determination of natural areas must engage the expertise of experienced field workers, if it was to be done satisfactorily. But while this was inevitable, the inherent susceptibility of such procedures to criticism on the basis of lack of objectivity was a matter of concern to Cain. And ecologists should have been, yet had not been, modest as to the ontological status of conclusions arrived at in this not entirely scientific manner. In Cain's opinion, the fact that subjective criteria were employed in the determination of associations on the ground brought into question the objective reality of the plant association in the abstract:-

> "I cannot see that the association, as usually understood in either the large or the small [i.e. in either the American or the European] sense, has objective reality."[56]

Note that the general form of argument used here by Cain was very similar in form to that we have already seen employed by Mason. The attempt at persuading ecologists to accept change took the form of an appeal to contemporary cultural criteria of what it was to be truly objective, truly scientific. The character of the discipline of ecology was contrasted with that of more secure, indubitably scientific disciplines (in Mason's case genetics and physiology, in Cain's physics, chemistry and mathematics). Ecology was found wanting. The implication was clear. Ecology must reform itself, become closer in methodology to those disciplines whose scientific status was not in doubt, if it was to enhance its own position within science as a whole.

In a mode of criticism often employed against theoretical orthodoxy, Cain called for more attention to be given to empirical data-gathering and naturalistic convention-free inquiry:-

> "There is a surprising paucity of information as to the exact areas of species and particularly on the composition structure and total areas of plant communities. I refer not to the hypothetical and admittedly approximate areas of "association types" according to the concepts of Clements for example but to actual concrete specific communities on the ground. One way of explaining what I mean is by reference to the differences between a cover-type map (as used in the sense of foresters to show actual vegetation) and an associational map, as often presented by ecologists purporting to show climaxes. The former objective type of map is needed by plant ecology. The latter may or may not result when abundant objective data are available."[57]

Like Mason, Cain called for a reassessment of the Gleasonian individualistic hypothesis:-

> "To the vast majority of ... ecologists ... bringing into question the objective reality of the plant association must seem heretical, today as it did to Nichols (1929) when he criticized Gleason's essay of twenty years ago on the individualistic association. For them it is the sine qua non of their science. The association is compared to the species. Just as a species is made up of the individuals of a kind, so is the association made up of association individuals ... However, believing that associations and species are not phenomena with the same objective reality, I wish to add my voice to the few, among them Gleason ... who have objected."[58]

Overall, Cain's condemnation of the state of the discipline of ecology was not as complete as Mason's. For instance, Cain maintained that it was important to retain, in their proper place, the traditional skills of the field ecologist:-

> "I wish to say plainly that no amount of physical data can ever suffice without the opinion of an experimental field naturalist in solving the problem of natural areas."[59]

The difference between the stringency of the two men's critiques is explicable in terms of the difference between their degree of attachment to ecology as it was then practised. Cain was much more a full member of the ecologists' community than Mason was. He was Treasurer of the Ecological Society from 1938 to 1940, becoming Vice-President in 1953 and President in 1958.[60] Mason had the outsider's freedom to make sweeping suggestions for reform. He had little investment in the practice of ecology as it then was. Cain, on the other hand, was an insider. He had a considerable professional commitment to ecology and it is thus understandable that he produced a less sweeping condemnation of contemporary practice.

Why, one might ask, did Cain advocate reform at all? Cain was, it should be noted, a very unusual sort of ecologist to find in America at this time. He had taken his doctorate under Cowles but had on several occasions taken time to discuss theoretical matters with Clements in Colorado and, as we have seen, with Gleason at the New York Botanical Garden. Such eclecticism was rare. Not only this, he also stood out from among his more parochial fellows by taking seriously the work of the European phytosociologists. He read the French and German literature and had tried out the European methods.[61] Cain also had research interests in floristic plant geography. And he was one of the earliest American ecologists to take an interest in the application of mathematics to the subject. He wrote the first American textbook to deal with quantitative techniques in vegetation science.[62] He thus had a range of experience and competence wider than that of many of his colleagues. Cain was flexible enough to accommodate certain changes in the practice of ecology and he was well placed to benefit from such changes.

Cain's extraordinary position was reflected in his personal standing among his peers. Despite his undoubted ability and energy, he was often regarded with a certain amount of misgiving by his fellow ecologists. His cosmopolitan eclecticism drew suspicions of dilettantism. As George Fuller put it:-

> "Cain is a good man but rather inclined to be carried away by every new doctrine."[63]

Nichols discouraged his students from reading and discussing Cain's work.[64] Cain was certainly an insider, when compared to Mason, but he was less of an insider than most.

Frank Egler's criticisms

The third of the critical trio of papers which appeared in the 1947 volume of Ecological Monographs was somewhat different from the ones already considered. Frank Egler's paper was not given at the Boston conference, nor was it, at least primarily, a theoretical review, as Cain's and Mason's were. That it appeared in the same volume as the other two was a coincidence. There was no direct consultation or collaboration between the authors. Egler had not been at the Boston conference. In 1947, he imagined himself to be virtually a lone protagonist for the Gleasonian point of view.[65]

Cain and Egler were both professional ecologists in the nineteen-forties. They were both aware of the discipline's problems. Furthermore their careers were linked in a more particular manner. They both had had sustained contact with Gleason. I have already noted, in the previous chapter, the importance of the New York

Botanical Garden as a focus for botanical activity in America. Gleason might have retired from active ecology, but in the Botanical Garden he was far from isolated. In the late thirties and early forties, Egler was frequently at the Garden, researching in its library.[66] He lunched at the staff table and happened to get a place next to Gleason's. Gleason, Egler recalls, was keen to discuss ecological matters. This was the beginning of a close association between the two men which was to last for several years. Eventually Egler, like Cain, was convinced of the validity of the individualistic hypothesis. Gleason came to regard Egler as a disciple.

Frank Egler's 1947 paper was a description of research he had undertaken on a previously unstudied area of vegetation - on the island of Oahu in the Hawaiian Archipelago.[67] Egler was as critical of the status quo in ecology as Mason or Cain had been, but in a somewhat different manner. He claimed to be able to support his criticism with new empirical evidence - the sort of new evidence that Cain had stressed the importance of, but did not supply. However, Egler's treatment of his vegetation data was not very novel. As far as his ecological practice was concerned, Egler offered the traditional descriptive observational style. He went out and looked carefully at the vegetation, described what he saw and arranged the plant communities according to what he surmised to be the important controlling factors and the processes of vegetational change.

Despite its appearing in a research paper, the principal thrust of Egler's attack was still at the level of theory. Egler expressed support for Raup and argued that circumstances were such that cognitive change would be timely:-

> "Science marches on, and American ecology appears to be on the threshold of fundamental changes in its conceptual structure. Old ideas have served their time. New facts demand new concepts, unless indeed we cling as the mediaevalists cling to Aristotle. Considerable dissatisfaction is being voiced with the ideas of the early twentieth century."[68]

Like Cain and Mason, Egler dissented from the community-unit theory as then conventionally employed:-

> "Personally, the writer believes the association-concept - valuable as it was at one stage in the history of vegetation science - to have caused serious confusions, and to have stymied the development of this entire field of knowledge. Because of certain connotations, the term association is not used in this paper."[69]

Egler refrained from employing not just one of the older key words, but three - not just 'association' but 'succession' and 'climax' as well. By refusing to employ their vocabulary Egler was, in effect, rejecting much of the legacy of the founders of American ecology. As we have seen in the last two chapters, the identification of succession and climax was the principal motif of pre-Second World War American ecology.

Egler asserted that questions of the direction of successional change have more often been settled "by faith than by empirical knowledge".[70] On the matter of the climax, he was agnostic:-

> "When the term and the concept were first presented, they served a very practical purpose. They represented to our then simple understanding of vegetation change, and in our simple northern vegetation, the one single and only end stage. The next two decades witnessed all sorts of limitations, encompassed by such learned verbosity as climatic, edaphic, physiographic, mono-, poly-, sub-, pro-, pre-, post-, dis-, and other climaxes ... At the present, the term covers a multitude of varying concepts for different scientists ... Until one or another of these concepts emerges with sufficient clarity to demand a term - climax or otherwise - I consider it best to refrain from the use of the word." [71]

Like Cain and Mason, Egler endorsed the individualistic hypothesis:-

> " ... the writer adopts wholeheartedly and without exception the "individualistic concept" of the plant community as developed by Gleason. In the light of the writer's knowledge of botanical literature, he considers these all-but-forgotten papers as being of top significance in the entire development of American vegetational thought."[72]

In short, Egler argued that it was time for a change and the individualistic hypothesis was an idea whose time had come.

Continuance of the Cooperian tradition

Ecology, in the late forties, was thus in a situation of suffering adverse scrutiny and damaging criticism from scientists both internal and external to the field. There are of course two standard strategies which one routinely finds used by actors in situations where the social order is under strain. I refer to the duality, familiar to us in politics, of reform versus revolution, the one continually attempting to thwart the other. If Egler, Mason and Cain may be taken as advocates of revolution - advocating radical alteration of the theory and practice of the discipline, seeking to discard rather than to renew the traditional systems, then on the side of orthodoxy and reform in this admittedly simplistic dichotomy, one might place Rexford Daubenmire of Washington State and Henry J. Oosting of Duke University, North Carolina. Both men had been students of Cooper at Minnesota; in fact they were doing their doctorates there when Egler was in Minnesota doing his Masters - in 1934.[73]

In the late forties, both Daubenmire and Oosting published textbooks in which they preserved the basic framework of their professor's work.[74] These texts were structured around the traditional descriptive approach to plant communities. They embodied the assumption of distinct vegetation types - to be recognised in the field by observation based on long experience and training. Unidirectional successions were assumed to change one form of vegetation into another, a process which culminated in the climax type. Climax vegetation was held to be determined uniquely by the climate. Neither Daubenmire nor Oosting explicitly rejected the mono-climax hypothesis - the hypothesis that all the vegetation within a single climatic area is successionally related to the highest or most mesic form of vegetation capable of growing under the given climate - despite the fact that their mentor Cooper, among many others, had been quite sharply critical of this aspect of Clements's theorising. Within this very traditional framework, there were, however, important concessions to more modern methodologies. Daubenmire and Oosting both emphasised the need for greater use of quantitative experimental and statistical techniques. Overall, these textbooks embodied a traditionalist, conservative, only mildly innovative stance.[75] They represented an attempt at continuity between pre- and post-Second World War ecology - as did the re-publication in 1949 of a revised edition of McDougall's textbook. In his new preface, McDougall wrote:-

> "Although many excellent papers and some books on ecological subjects have been published during recent years, most of them have not changed our fundamental thinking to any great extent."[76]

These three textbooks were not liked by Egler. In 1951 he reviewed all three together and was moved to write some of the most vehement criticism ever produced by a writer who was never one to pull his punches:-

> "The comments on these books are not to be considered primarily a review of their factual contents and a spotlighting of the good and bad in omission and commission. To the contrary, the comments are in the nature of a critical analysis of certain methodologic and epistemologic foundations of American ecology. The immaturity and artlessness of some of these foundations deserve serious scrutiny in these times that have seen the rise of Nazi physics and Soviet genetics. As Americans, we bugle our claim that totalitarian straight-jacketing of the scientific intellect destroys science. It follows as a corollary that freedom of the scientific intellect is a precious privilege and those who possess it have a deep obligation to exercise it for the advancement of science. It comes as a curious anomaly therefore to find evidence of a self-imposed imprisonment on the part of some scientific workers, with apparent contentment on their part ... There are many men whose ideas and habits of thinking are so firmly ingrained that neither the clearest logic nor the subtlest persuasion will lead them to reconsider their viewpoints."[77]

Egler invoked the Clementsian system as an example of what must be avoided:-

> " ... we have Clements, the uncompromising idealist, the speculative philosopher, driven by some demon to set up a meticulously orderly system of nature, as neatly organized and arranged as the components of Dante's Inferno ... The climax is identified with climate and physiognomy, thus supplying two of the most characteristic features of the Clementsian speculative philosophy. We are then subjected to an orderly breakdown of the climax carrying us through a sequence of -ations, -es and -ules of associ-, consoci-, faci-, loci-, soci-, lami-, and sat-'s, in all their devious combinations."[78]

Egler admitted that Daubenmire and Oosting's texts were fair and competent, if restricted, re-expressions of "what has been to them the changeless philosophic structures they learned as students".[79] But Egler reiterated the arguments he had made in 1947 - new circumstances demanded change and a departure from old ways of ecological thought:-

> "Sciences ... go through long periods of patient plodding accumulation of data. These are tacked onto the basic framework of the science, until sometimes it groans with the burden of carrying such a multitude of minutiae. Then suddenly there is revolution, an upheaval ... a new structure appears based on entirely new concepts ... Some American ecologists however have felt they have attained "reality" and all that is now necessary for themselves and their students (who have inherited the sense of finality) is to go on adding details to the old conceptual structure. Thus American ecology has been stuffing itself with such "facts" for half a century, and in the neatly appropriate year of 1950, it is showing some cracks in its chitin." [80]

These sweeping and fundamental condemnations and criticisms struck home. Egler recollects that whereas Oosting eventually forgave him, Daubenmire never spoke to him again.[81]

A noteworthy feature of Egler's 1951 polemic against the contemporary state of American ecology is that he adopted a form of argument similar to that found in Cain's or Mason's 1947 paper. He made a damaging contrast between ecology and more prestigious disciplines. His advocacy of radical change was likewise predicated upon the appeal to culturally-given criteria of what it was to be scientific. Egler, however, adopted a different paragon subject. Rather than reflect upon ecology's deficiencies as compared with particular scientific disciplines, such as genetics or chemistry, Egler chose to contrast it with the one ideal scientific discipline, that ultimately prestigious one - the one invented by philosophers of science. Not surprisingly, ecology is again found wanting:-

> "There exists also a remarkable naiveness toward our European cultural heritage in the realms of scientific methodology, applied logic, and the philosophic foundations of the exact sciences ... This innocence of the principle of scientific methodology is more insidious than appears at first glance ... until such adults ... are willing to settle down and really think along unaccustomed channels, they may continue to thwart

> the development of American Plant Ecology. To speak more concretely, the traditional ecologic theories were not proposed and tentatively accepted, and verification was not attempted by methods of logical analysis."[82]

I think it is fair to say that generally disputes within ecology at this time were not as acrimonious as the above passage from Egler would suggest. But Egler's 1951 review and his 1947 paper, taken together with Cain's and Mason's articles, are evidence that there were real divisions and strains within American ecology in the late nineteen forties and early fifties. Accepting the existence of such divisions, one might ask why Daubenmire and Oosting were on the side of tradition and only relatively mild innovation.

Daubenmire and Oosting were typical middle status academics.[83] Both had had perfectly standard apprenticeships - both had been students of the most mainstream of all the major teachers in the field - W.S. Cooper. Cooper had not been damagingly close to Clements, nor damagingly out of step with ecological orthodoxy more generally. He was, as far as I have been able to discern, universally respected. Attempting to work within his legacy must have seemed a tenable strategy. Neither Daubenmire nor Oosting had well-developed competences in any other fields, nor did they have experience of ecological practice outside the United States.[84] They were thus thoroughly socialised toward orthodox professional ecological practice. They were not equipped to reform the discipline by importing techniques from other disciplines or research programmes. Both had had a long period of initial career uncertainty between leaving graduate school and gaining permanent employment.[85] But in the nineteen forties both were beginning to reap the standard rewards of normal academic careers. Oosting had just been made a full professor and had been appointed to the editorial board of the journal Ecological Monographs. Daubenmire had become established at Washington State University and was beginning to be appointed to various committees of the Ecological Society. There must have been little incentive for them to rock the boat.

Furthermore, they were both very good practitioners of the old style of investigation. Daubenmire's papers are especially noteworthy in this respect.[86] They constitute perhaps the finest American development of descriptive ecology based on the community-unit theory. The whole exercise was firmly based on classificatory techniques. Types of vegetation were identified and delimited by observation and experience and characterised in detail by quantitative species lists taken from specially selected plots. The occurrence of vegetation types was correlated, often quantitatively, with environmental and biotic factors. Successional relations were determined by extrapolation. All combined to give a vivid and comprehensive understanding of the vegetation under study. It is not surprising that scientists capable of producing such studies should have an interest in preserving and maintaining the cognitive status quo - which gave meaning to this mode of investigation.

Egler, on the other hand, did not have a permanent job and did not conspicuously appear to want one. His radically independent turn of mind was conveniently connected to a degree of financial independence.[87] He and his wife owned a thousand-acre estate in Northern Connecticut to which he often threatened to retreat. He had professional involvements in applied ecology, range management, and consultancy work, all of which lessened his career investment in pure plant ecology.[88] Egler was well-placed, as a comparatively marginal, comparatively independent figure, to criticise and to point to new directions for the discipline.

Egler cannot be said to have been successful in his task of reform. His suggestions had little direct effect on ecologists' practice. When the discipline did change, he was not in the van of these developments, nor was he held to be their inspiration. To some extent, Egler's carefully cultivated independence worked against him. He was regarded as being eccentric, unorthodox and not a little troublesome.[89] His papers were most unconventional in style and he refused to allow editors to alter them.[90] His writings clearly show his critical distance from the rest of the profession. He was not sufficiently a member of the team to become its new leader. Also, and perhaps more importantly, despite the unconventional manner in which he presented his results, his research methods were still virtually those of the old-fashioned solitary field naturalist. His practice was based on observation and description of vegetation and on skill at species identification. His interpretations of vegetational processes were couched in terms of his personal experience of vegetation. He was not a great quantifier, using statistics only seldom and other forms of mathematics not at all. In this respect his practice was less innovative than Daubenmire's and Oosting's. He employed little in the way of investigative technology or elaborate experimental methods. He was well read in the philosophy of science, but however strongly he might be able to defend his subjective methodology as truly scientific in philosophical terms, his actual practice did not look much like that of a successful modern biologist. He once described himself (not explicitly but the implication was clear enough) as a Prince of Serendip.[91] In the dawn of the new age of Big Science and Organization Men, the Prince of Serendip was not likely to be much of a Pied Piper.

Similar arguments might be made as to why Cain or, _a forteriori_, why Raup (two other _enfants terribles_, although perhaps less _terrible_ than Egler) did not lead the transformation of plant ecology. In hindsight, it seems that what was required was not theoretical or logical argument or generalised methodological prescriptions, but new forms of practical procedure. When the theoretical reform came it was mediated by new investigatory techniques - techniques which were so designed as to resemble those employed by more prestigious biological disciplines. The new exemplar changed theory and practice together and changed both in strategically relevant ways - ways determined by culturally given criteria as to what it was to be scientific.

New empirical work: R.H. Whittaker

Unbeknown to Cain or Egler, a study which did involve new methods of field investigation was already underway. Robert H. Whittaker, a graduate student at the University of Illinois, undertook, in the summer of 1947, an intensive study of the vegetation of the Great Smoky Mountains in Tennessee. Whittaker was aware, on beginning the project, that there existed a diversity of opinion as to the nature of the fundamental units of vegetation.[92] Whittaker's principal supervisor was Charles Kendeigh, a zoologist who worked with a notion of the community-unit similar to Clements's.[93] Whittaker had also been taught at Illinois by Victor Shelford whose collaborative connection with Clements I have detailed in Chapter

Two. Whittaker had however read widely and was aware that the European phytosociologists employed units of a different kind. Furthermore, his second supervisor was Arthur Vestal, Gleason's former research assistant. Vestal had remained what one might term a crypto-Gleasonian.[94] He introduced Whittaker to Gleason's work and to the individualistic hypothesis.[95]

Whittaker went to the Great Smokies determined to devise an objective test that would discriminate between the various theories of species grouping in plant communities. The technique he devised was random sampling - placing his sample plots within the vegetation not with a view to illustrating vegetation types, but to sample the vegetation as a whole.[96] Whittaker did not set out primarily to classify the vegetation of his study area:-

> " ... methods free from the subjective difficulties of conventional ecological procedure were sought in order to analyse the vegetation without reference to preconceived "associations"."[97]

This was a radical departure from the accepted norms of field procedure. Random sampling of vegetation had never been done before in America.[98] One factor which facilitated Whittaker's adoption of new techniques was that he had not been thoroughly trained in the practices of traditional plant ecology:-

> "It [random sampling] appealed to me, first because it was more objective ... Also I didn't know what the natural types were, therefore how could I, why should I, try to sample in terms of them?"[99]

Whittaker was a graduate student of zoology. The thesis project was originally intended to be a study of the foliage insect communities of the Great Smokies.[100] Whittaker recalled that it was almost inadvertently that the preliminary survey of the vegetation grew so large that it eventually constituted the final thesis by itself.[101]

Using the technique of random sampling, Whittaker came to the conclusion that none of the various theories as to the nature of the community-unit were correct:-

> "In the course of the vegetation analysis the author felt himself compelled by his data to accept fully the individualistic hypothesis of Gleason, and to seek new

ways of constructing an understanding of communities from an individualistic beginning."[102]

Whittaker recalled that he came to this conclusion before he was aware of the fresh support given to Gleason by Cain and Mason:-

"Independent and simultaneous - you can say what you like about the time being ripe for this."[103]

In his description of the vegetation of the Great Smokies, Whittaker described a pattern of continuously changing species composition, along environment gradients - in this case, the obvious ones of elevation and exposure. There were no definite vegetation classes. Species distributed themselves individualistically, each with its own maxima at a different point along the gradient. Substratal species, shrubs and herbs, distributed themselves independently of the dominants.

Whittaker coined the term 'gradient analysis' to describe his new approach to vegetation:-

"Gradient analysis seems one of the most fruitful and realistic means by which vegetation can be studied. By it the investigator can free his study from the difficulties of pre-conceived associations and work in terms of one aspect of ecological reality - the actual distributions of community members in the environment and their relative status in different communities."[104]

As a graduate student, Whittaker had very little background in statistics or mathematics.[105] Nevertheless one of the attractions gradient analysis had for him was its inherent quantifiability and its statistical nature:-

"These groups ... show distribution of trees by their percentages of the stand and of the canopy against the primary gradients of elevation and site moisture-balance. The isa-rhythms [sic] of percentages drawn outline the binomial solids, the distribution-forms described as peaks and ridges, and show their relation to one another, to the gradients and their interaction, and to the major communities. The most impressive features of this series of charts are, first, the apparent universality of binomial solids or some modification of them as the basic distribution pattern, and second, the general distributional independence of different species."[106]

Gradient analysis would banish subjectivism from ecology:-

> "Daubenmire was saying that because you can see what looks to the human interpreter like a discontinuity, there has to be a discontinuity there and your method is wrong if you can't show that. What I think I see is correct. Of course it's not so - we see what in many cases appear to be well-defined zones on mountains from a distance but when we study them in detail they intergrade with one another. The findings of quantitative analysis are necessarily stronger than the visual impressions of discontinuity."[107]

Furthermore gradient analysis promised the development of a truly qauntitative ecology:-

> "The techniques we have been using have become increasingly mathematical, as we have been seeking more objective, more efficient, more accurate ways of dealing with vegetation. I think that would be the major change in this area of research."[108]

Further evidence that the change Whittaker was advocating for the discipline was one which would bring its character nearer that of more prestigious botanical disciplines is afforded by noting whence Whittaker first received support for his new ideas. Whittaker was well aware of the radical nature of his dissent from conventional plant ecology:-

> "I felt very alone - in a position for which Gleason had been castigated."[109]

He was grateful, therefore, for the support he received from Wendell 'Red' Camp:-

> "Red Camp found out about my work, was very interested in, and was an enthusiastic supporter. The individualistic hypothesis fitted in with the way he liked to see things. So, yes, I had extensive contact and support with him."[110]

Camp's support for Whittaker began very early - in 1947[111] Camp was not a plant ecologist. He called himself a biosystematist.[112] He was among the first to develop a genetic understanding of the segregation of ecotypes. The biosystematists employed the new Mendelian genetics to interpret floristic distribution and species variation in the field.[113] This was a rapidly developing research programme at this time. Camp and his fellows were doing what we have seen Mason advocating in 1947 - interpreting population phenomena in genetic and physiological terms.

Camp had worked in the Great Smokies.[114] He thus understood the floristic and vegetational background to Whittaker's work. Furthermore, he was, at this time, a member of staff of the New York Botanical Garden. He knew Gleason well and he had had many discussions with Gleason on taxonomic and ecological matters.[115] Camp saw the possibility of using the individualistic hypothesis to achieve an understanding of communities in terms of population genetics. This was very similar to what Whittaker intended:-

> "I think, myself, that the future of field plant ecology lies along the lines of population analysis which I am developing and which others of my generation will work out."[116]

Whittaker had thus created an ecological theory which harmonised with the prestigious Neo-Darwinian synthesis, and which Camp was, for several reasons, well placed to understand.

However, a new form of investigatory practice, fresh data, and good relations with fashionable disciplines were necessary but not sufficient conditions for the successful reform of plant ecology and the general introduction of the individualistic hypothesis. Whittaker was at the wrong end of power relations within the discipline.

Whittaker was young. He had done his radical new work while a graduate student. He was to have difficulties finding a satisfactory job and getting his Smoky Mountain work published.[117] The Ph.D. thesis was examined and accepted in 1948 but the material was not published until 1956.[118] After several false starts, Whittaker submitted a manuscript to Ecological Monographs:-

> "I had substantial trouble with the editor, who was H.J. Oosting. I would, in retrospect, concede that Oosting was doing his best to deal fairly with me and that the troubles, as an author, were primarily myself. But anyway it was a long negotiation to get that through some adverse reviews ... I was getting some adverse reviews because what I said was unpalatable to conservative ecologists."[119]

The main sticking point was, ostensibly, the new sampling technique:-

> "I was told by Daubenmire, for example, that it was not scientifically valid to sample the way I had done because one would get a lot of stands that were intermediate or disturbed and were inappropriate to the recognition of the types one was trying to seek and demonstrate."[120]

A sampling technique which was not designed with the asummption of community-units would not inspire the confidence of a community-unit theorist and therefore would not count as an objective test. Whereas Whittaker appealed to criteria of objectivity pertaining outwith plant ecology, traditional ecologists appealed to criteria internal to the discipline. The two were quite different.

A certain amount of ill-feeling was aroused:-

> "These men, remember, had devoted themselves to a lifetime of research on vegetation, using a certain set of assumptions and for me to come along and challenge their assumptions did not please them."[121]

J.T. Curtis enters ecology

In the late forties and early fifties, Whittaker was not poised to lead a reform of ecological theory and practice. However, again quite independently, another investigation of the basis of the community-unit theory had begun. The principal mover of this, John T. Curtis, was more successful in attracting favourable attention and acceptance. The work of Curtis and his associates established the individualistic hypothesis upon a new quantitative base and gained for it a central position in American ecological theory.

John Thomas Curtis was born in Waukeska, Wisconsin in 1913, and attended Carroll College in Waukeska.[122] He displayed an interest in natural history from his high school days, becoming a protégé of the Milwaukee Museum's Botanical Curator, Albert Fuller.[123] He published three short papers while still an undergraduate at Carroll.[124] One of these was a contribution to floristic botany, recording his discovery of a new hybrid of the native Wisconsin lady-slipper orchid, Cyripedium. The other two were on ornithological observations. Judging by these early papers, it is safe to assume that Curtis had already gained considerable competence in natural history before starting his graduate training.[125]

Curtis graduated A.B. from Carroll in 1934 and went on to the University of Wisconsin, Madison, where in 1935, he gained the degree of A.M. Curtis's graduate research was directed by the most eminent botanist active in the University of Wisconsin at that time, Benjamin Duggar. Duggar was a plant physiologist and phytopathologist of international renown.[126] Curtis worked for his master's degree and his doctorate under Duggar on the general problem of orchid seed germination. The study was directed along three main lines:- environmental influences on germination, seedling nutrition, and mycorrhizal relations. Investigation of the last formed the most detailed part of the thesis. Several aspects of orchid mycorrhiza were studied including the distribution of the fungi and the degree of specificity between fungal species and the species of host orchid.

While a graduate student, Curtis also worked with Dr. Alexander Hollaender, a colleague of Duggar's, on the effect of ultra-violet radiation on micro-organisms.[127] It should be noted that Curtis's physiological investigations, while lacking nothing in technical sophistication by the standards of the nineteen thirties, were not narrowly conceived laboratory studies. On the contrary, his research involved a certain amount of field work and aspects of it were, at least potentially, relevant to ecological questions. This broad conception of physiological inquiry is in contrast to the narrow scope of much physiological work being done at the time, but it should not be thought of as in any way peculiar to Curtis. It was typical of the style of botanical investigation promoted and sponsored by Benjamin Duggar, who sought to make physiological research relevant to the life of the plant as a whole.[128] In this regard, Duggar was interested both in agronomy and applied biology, on the one hand, and in environmental physiology on the other. Duggar's concern with environmental science is further evidenced by the fact that in 1938, he, together with Norman Fassett, set up the first plant ecology course ever to be taught at Wisconsin. This was the year after Curtis gained his doctorate and he now held the post of instructor in the Botany department. He was Duggar's assistant and Duggar encouraged him to help with the teaching of the plant ecology course.

While still a student of Duggar's, Curtis was also involved in another line of work in which the ecological and the physiological were intimately combined. He spent his 1935 summer vacation as botanist in charge of photosynthesis work at the Trout Lake Limnological Laboratory of the Wisconsin Geological and Natural History Survey. The University of Wisconsin, at this time, was the home of a very important programme of limnological studies, which constituted the most advanced research into the fresh-water habitat then being undertaken in North America.[129] These studies had begun with the work of E.A. Birge, and had been continued under the general direction of his collaborator, Chancey Juday, who in 1931 became Professor of Zoology in Madison.

In the 1930s, Juday began to turn his attention away from descriptive limnology and towards measurement of the rate of energy fixation and the subsequent transfer of energy between the trophic levels of a lake. During the summer of 1935, Curtis worked with Juday upon experiments designed to determine whether algae in their natural habitat had photosynthetic productivity similar to those of cultured algae in the laboratory.[130] This work, published in 1937, was one of the first bioassays of productivity in the field.[131]

In 1940, Curtis was granted a semester's leave of absence to go to the University of Pennsylvania and set up there a physiology course of the type that Duggar taught at Madison. The Botany Department in Madison was eager to have him back, and by the end of 1940 he had returned, this time as an Assistant Professor. Experimental physiology still formed the major part of his research effort, but he was steadily developing his interest in ecology.[132] In 1941 he took over Duggar's half of the teaching of the plant ecology course, and in the same year he founded a course entitled "Problems and methods of plant conservation". This was the first course in conservation in the Botany Department at Wisconsin, a university which was already involved in conservation studies with the work of Aldo Leopold who held a chair in Wildlife Management and was a close friend of Curtis.[133]

In 1942, Curtis joined the Ecological Society of America. He had not yet published his first paper on a purely ecological subject, but he was more actively engaged in ecological research than he had been before. He had extended his work on the native orchids to include study of the plant assemblages within which the orchids grew, so as to be able to relate studies of their physiology and autecology to their synecological context - again to make the physiological inquiry more ecologically relevant. Also, among several other projects in physiological ecology, his experience with mycorrhiza was being employed in an investigation of the problems involved in the artificial regeneration of pine forest. These involvements in ecological research may be considered as more or less natural extensions of his earlier work in physiology. They were all applications of his physiological expertise within an ecological context.

In the early nineteen forties Curtis made a distinct shift in the emphasis of his research - away from the physiology, pure or environmentally applied, which characterised his early research, towards mainstream community ecology. We can see this from the fact that, in 1941, Curtis applied to the Guggenheim Foundation for a fellowship to allow him to investigate, full-time for a year, the phytosociology of the Lake Forest. This project represented a new departure for Curtis, since the proposed investigation would not involve the application of physiological expertise to an ecological problem. It was rather a research topic entirely within vegetation science. Curtis intended spending his Guggenheim year with W.S. Cooper in Minnesota.

Curtis thus entered the ranks of plant ecology already with an established reputation in the more prestigious field of physiology. And yet, it is important to note, Curtis also possessed an interest in natural history, well-developed and of long standing, a talent for work in the field and experience of ecological problems. He was this well-equipped to adapt quickly to his new intellectual environment.

Curtis came into ecology with a mission to cleanse the stables, "to go far toward establishing ecology as a science instead of an art".[134] He desired an ecology that was "scientific, with rigorous requirements based on quantitative data".[135] As a physiologist he was well aware of what were the culturally given criteria of science. These were the standards to which ecology must adhere.

Curtis's entrance into ecology was delayed. He was not long into his Guggenheim Fellowship at Minneapolis when his plans were affected by the involvement of the United States in the Second World War. With the capture of the Malaysian plantations by the Japanese, the Allies were in danger of suffering a serious shortage of rubber. Alternative sources were urgently sought. In Haiti, the United States Emergency Rubber Project was set up to investigate the rubber production potential of species of Cryprostegia. Curtis was made its Research Director.

Curtis remained in the Caribbean until 1945, and it was not until late that year that he returned to Wisconsin. This enforced migration produced important intellectual consequences. In Haiti, Curtis gained experience of exotic vegetation. He undertook a study of the palo verde woodland.[136] Also he came into contact with experts in tropical botany, notably Lester R. Holdridge.[137] Curtis found the ideas of plant communities which he had gained in temperate America difficult to apply to tropical vegetation.

On his return to Madison, he wrote to Cooper to say that he no longer intended to continue with his Guggenheim project. He no longer saw it as a feasible or worthwhile piece of research:-

> "I find myself with markedly different views concerning the general field of plant ecology than I had when I was last in Minneapolis. First hand study of the immensely complex group of tropical plant associations has more or less undermined my faith in the possibilities of arriving at any clear-cut conclusion regarding the relationship of our own seemingly simple plant societies. The disillusionment, in fact, has been so great that I now entertain serious doubts concerning the validity of the entire plant-association concept. In other words, the idea that any considerable numbers of plant species possess environmental requirements sufficiently alike to permit them to form sociological units, having definable and meaningful composition, structure and development seems to me highly debatable. At least, I am convinced that no meaningful definition can be forthcoming until we have far greater knowledge concerning the requirements and the behavior of the individual species than we now possess."[138]

Curtis conceived a grand plan to put matters right. By the end of 1946, he had embarked upon several long-term studies, or rather a single long-term project with several aspects. Curtis, skilled at raising research grants, persuaded the Wisconsin Alumni Research Foundation to fund a ten-year project aimed at describing and investigating the vegetation of Wisconsin. This support provided not only research money for Curtis and other faculty members working with him, but also financed a steady stream of graduate students. Curtis also attracted research funding in smaller quantities from several other sources. Quite quickly a considerable team of workers gathered around Curtis in Madison.

In the ten-year period from 1946, ten Ph.D.s and nine M.S. degrees were awarded to graduate students associated with the project.[139] All worked on topics picked for them by Curtis. Each played a role in the overall plan. Grant Cottam, a graduate student until 1948, joined the faculty in 1949 and continued to work closely with Curtis. Several other members of the Botany department, including Norman Fassett and Henry C. Greene, were also involved in aspects of the research.

Curtis was a skilful and inspiring project director:-

> "He was very much the leader and you wound up after you got an education under Curtis being a disciple ... The graduates were a closely-knit group. They liked Curtis. We all met together once a week for lunch - and it was friendly half-social, half-business ... He was an excellent teacher and he spent hours and hours with the graduate students - each of them had a one hour appointment every week. He kept their nose to the grindstone."[140]

New techniques

One of Curtis's great concerns was methodology. Methodological innovation was necessary to establish "ecology as a science instead of an art".[141] A considerable advance was made in 1947, when Curtis and Cottam successfully applied the surveyor's method of 'random pairs' to the sampling of forest vegetation.[142] This technique allowed quantitative data on woodland to be generated much more quickly than ever before:-

> " ... we had methods where one man could go out and sample, say, four stands in a day and in the course of a summer collect data on a hundred or so stands. Because of this we had a lot more data to work with. Up to that time most of the papers had been written

over a single stand or two or three stands. But Curtis immediately put his students to work gathering data on lots of stands."[143]

The quantitative techniques developed by the European phytosociologists were studied, modified and applied to the grassland vegetation of the state.[144] Curtis and his students pioneered the use of punched cards and computing machines for the storage and manipulation of vegetational data.[145] Field experiments on the effect of fire and perturbation upon study plots were undertaken in the University's Arboretum.

In 1947, upon submitting the results of an early series of these experiments to Ecology, Curtis experienced some difficulty in getting the material published:-

> " ... to judge from the reviewers' comments they objected not on the basis of how the material was presented but rather on what was said ... This is not the first indication I have had that our Wisconsin idea of learning about the dynamics of plant formations through their experimental manipulation ... is a little ahead of its time ... We are not discouraged but will proceed according to plan ... In future we will restrict our papers for "Ecology" to those dealing with traditional descriptive ecology since we do carry on such work as a necessary adjunct to the experimental establishment program."[146]

The paper was eventually published by the American Midland Naturalist.[147]

Curtis did not have such troubles often. He was an experienced author, having already published many articles in the physiology journals, and he knew how to please the editors of periodicals.[148] After 1950, the Wisconsin school had little difficulty getting their papers published.[149] The iconoclastic Whittaker, by contrast, was still having chronic problems getting some of his material published as late as 1960.[150]

By 1951, Curtis was on the editorial board of Ecology and able to exercise his influence not only to get innovative material into the journal, but to keep old-fashioned work out and to impose his standards upon the discipline. Indeed, he did not confine the exercise of such influence to Ecology. In 1959 he wrote to Oosting, the editor of Ecological Monographs:-

"I cannot resist the urge to write you and complain bitterly about the publication of Martin's paper on Algonquin park in the new monographs. This is the worst piece of ecological tripe I have read in years. How did it ever get by your editorial board? It is filled with unsupported assertions, contains only limited data from single stands chosen with a preconceived view in mind ... To me it does not seem right to open the pages of our journals to the exposition of hare-brained ideas that are totally unsupported by the evidence. We all have a responsibility to see that ecology remains scientific, with rigorous requirements based on quantitative data. This paper fulfills none of the requirements."[151]

New theory - the continuum

One of the first of the graduate students Curtis put to work on the random pairs sampling method was Robert P. McIntosh.[152] McIntosh recollected that the ease with which data could now be collected rendered possible a new approach to vegetation sampling:-

"A good part of the whole approach was that you got lots of data ... The distinction I am sure was quite clear in our minds that against the older approach whereby you classified subjectively and then went in and sampled your pre-classified groups as representatives, put these together as descriptive of what you had already classified - this kind of approach [random pairs] allowed you to put things together come what may rather than simply describe what you have previously classified."[153]

Using the quadrat method a sample of woodland might take a week or more to complete. Therefore each sample had to be carefully placed so as to be optimally useful. When more than one could be done in a day, the investment in each was less. Sample plots could be placed more speculatively, with less of a fixed idea in the investigator's mind as to what each was intended to display.

It was clear to the Wisconsin group that their early attempts at classification had been arbitrary and, hence, unsatisfactory.[154] They had few guidelines on which to work. Curtis had newly become an ecologist - when McIntosh arrived in Wisconsin in 1946, he was still teaching physiology. His ecology was largely self-taught - he had no developed system of classification to introduce his students to. Indeed, he was sceptical of all the existing systems.

The examples of classification in the ecological literature were not precise or detailed enough to function as working models:-

> " ... in the literature, of course, there were fairly explicit descriptions of oak-woods, maple woods, actually several kinds of oak-woods and as I went around and qualitatively tried to figure how these things fitted in - then it was just very difficult - because none of these papers spelled out the criteria - they generally don't - they are more or less like and so on."[155]

So, like Whittaker in the Great Smokies, Curtis's students worked without a detailed image of what the constituent associations in their study vegetation might be. Unlike Whittaker, they did not deliberately set out to sample at random.[156] But they were able to sample more freely and speculatively than ever before. This had a similarly disorganising effect on the data produced. They had, as McIntosh recognised, a distinctively different approach - an approach which, by its very nature, produced large amounts of data - data which would not fit into any existing scheme of vegetational classification.[157]

Curtis and McIntosh were, thus, faced with a problem. How were they to organise into a publishable form the large amounts of data that the new sampling technique had generated?[158] In 1948 and 1949, McIntosh worked on the problem:-

> " ... one of the first approaches we took was the mechanical strip method. It's just a big board with a little strip across the bottom and we cut long narrow white plastic strips and then marked quantities and then basically just lined them up and shuffled them back and fore - trying in effect optimally by eye-balling to see how the species distributed. Since it was the old tradition that black oak was the one end and sugar maple was the other, so we generally started out like that. I was doing all the mechanics of this because John had lots of other things to do. But we put the black oak at one end and the sugar maple at the other and saw how the others fell. And then juggled them to optimum - to see whether you could make the smoothest curve. You got pretty thoroughly into the series of patterned curves. Then with all the tree species you got the continuum-type sequence."[159]

In other words, the best way to organise the stands appeared to be into a sequence of continuous variation, each dominant gradually peaking in frequency, and then dropping out along a continuum between stands dominated by sugar maple, Acer saccharum and stands dominated by black oak, Quercus velutina. There were no distinct 'associations'. Each species had its optimum occurrence at a different point on the scale.

This idea of an 'upland forest continuum' without definite classes within it was first presented by McIntosh and Curtis at the meeting of the Ecological Society in Columbus, Ohio in September 1950.[160] The paper attracted little comment. The most remarkable event of the conference for Curtis was his discovery that Whittaker was working along similar lines.[161]

Later in the same year, Curtis and Cottam went to another meeting in Cleveland to present related material:-

> "I remember that Curtis was very apprehensive when we went to Cleveland ... He expected to be attacked. He expected we would both be attacked, we both gave papers. But we weren't."[162]

The McIntosh and Curtis manuscript on the upland forest continuum was readily accepted by Ecology and appeared in the summer of 1951.[163] Meanwhile in Madison, Curtis's students were being set the task of applying the idea of the continuum to other types of vegetation. A total of nine papers were presented by Curtis and his students to the 1951 Minneapolis meeting of the Ecological Society.[164] Four of these described new continua. Again there was little controversy. Curtis was not altogether pleased by the calm reaction to the Wisconsin work:-

> "In fact we were badly disappointed at the recent Minneapolis meeting at finding very few who either agreed or disagreed. We were beginning to think that our work was making no impression of any kind."[165]

Curtis was a forceful public speaker and formidable in argument.[166] All his papers, and those of his students, were very carefully prepared and presented. He was not an opponent to engage with lightly. Furthermore, his approach was more quantitative than was then standard, and doubtless this inhibited comment from mathematically-unsophisticated audiences. However, one of the most important factors in easing the acceptance of the Wisconsin work seems to have been a widespread confusion as to what the continuum actually referred to.

As described above, the upland forest continuum consisted of a series with black oak at one end and sugar maple at the other. This was 'traditional', as McIntosh put it, because the black oak was regarded as being a xeric, pioneer species and the sugar maple as being a more mesic, climax species. Thus the two ends of the Wisconsin continuum coincided with the two ends of a perfectly conventional successional series. Furthermore, much of the vocabulary with which Curtis and McIntosh described the upland forest continuum was borrowed from the language of successional theory:-

> "The sequence of the species in this pattern is such that pioneer species are at one end and climax species at the other ... The results of this study ... indicate that Acer saccharum is the tree species best equipped to persist in the terminal forests of the area. All other species are less efficient in this respect and their relative degree of 'climaxness' may be evaluated by the spatial relations of their optimum development curves ... "[167]

The position of species along the continuum was referred to by 'climax adaptation numbers'. In one schematic description of the continuum, the species were connected to one another by arrows which lay in the same direction as, under Cowlesian and Clementsian theory, progressive successional change was held to occur.[168]

Thus, despite the explicit support voiced by Curtis and McIntosh for the Gleasonian hypothesis and despite the lack of any explicit mention of dynamic relations between the stands, the 1951 description of the continuum lent itself to the interpretation that what was being characterised was not a continuous series within climax forest, but a sere between pioneer and climax vegetation. That seres were at least occasionally continuous was an accepted part of orthodox ecological theory. Thus it was easy for the traditional ecologist to interpret Curtis's work as a very elegant quantitative description of a continuous sere. This seems to have been the basis on which the paper was accepted by D.B. Lawrence for publication in Ecology:-

> "I would suggest that you reconsider the use of the term "ecological adaptation number" [later changed to climax adaptation number] which seems to me ambiguous and could mean almost anything. Why not call that idea the "sere number" or "succession number"?[169]

Whittaker, on the other hand, by continually emphasising the mature, undisturbed climax nature of the vegetation he studied in the Smokies, denied the traditional ecologists the opportunity of accepting his work as a description of a continuous succession.[170] Whittaker confronted orthodox theory earlier and more directly than Curtis did.

Lawrence was not foolishly or gratuitously misunderstanding Curtis. I would argue that the Wisconsin group itself took some time to decide on the status of the continuum. In 1949, Curtis seems to have thought of it principally as a description of succession:-

> "We have erected a succession index for the purpose of classifying upland hardwood on a scale varying from pioneer species on one end to climax species on the other."[171]

Even as late as 1956, Curtis still regarded the upland forest continuum as, at least partly, a description of a dynamic process of succession:-

> "You are right in your assumption that most of the types in the continuum are not permanent but will be followed by others higher on the scale in the absence of disturbance. The terminal forests (climax, if you will) on the other hand tend to change much more slowly, always in the direction of sugar maple."[172]

The idea of the continuum as a description of continuous variation between mature climax stands emerged only gradually. Like the development of the idea of the community-unit described in the first chapter, the discovery of its antithesis, the continuum, was a process, not a unit-event. It emerged only gradually from McIntosh and Curtis's deliberations over their board and their plastic strips. And, for a long period, the distinction between the continuum and conventional descriptions of succession was blurred. The early expressions of the continuum idea contained successional connotations. These connotations allowed adherents of the community-unit theory to interpret Curtis's results as compatible with their own views on vegetation. It seems that this defused much potential controversy, allowing the Wisconsin work an easier passage than it might otherwise have experienced.

In 1955, in the published version of the prairie continuum paper, Curtis explicitly stated that a continuum existed between mature climax vegetation stands. Having described a continuous variation between dry, mesic and wet prairies, he maintained:-

> "There is no evidence whatever that the wet prairies are capable of becoming mesic prairies through any reaction their members may have on the habitat, nor can the dry prairies so change their environment as to become mesic."[173]

In other words, the continuum was no longer associated with successional change. It had come to be regarded as a distinctively different phenomenon.

Articulation of the continuum exemplar

In 1952, Curtis gave a paper on the continuum idea at a symposium in St. Louis, organised by Stanley Cain. The prominence which Curtis had already achieved as an opponent of the community-unit theory is clear from Cain's invitation:-

> "It is obvious that such a matter [vegetation classification] can't be handled in any adequate manner without the continuum being represented. And the continuum can only be adequately represented by John T. Curtis."[174]

Whittaker was not invited to speak at the symposium. Whittaker's 'gradient analysis' and Curtis's 'continuum' were virtually identical concepts.[175] But Wisconsin had become identified as the sole source of the new approach. Cain described Curtis as "the father and leading exponent of the concept of the continuum".[176]

In the 1952 symposium, Curtis was able to refer to studies, undertaken upon a large variety of vegetation types, which supported the continuum theory. Continua had been found not only in the southern hardwood and the prairie, but also in the northern coniferous forest, the herbaceous understory of both coniferous and hardwood forest, among epiphytic lichen and soil fungi.[177] There was even a study of the continuously varying distribution of nesting birds.[178] Curtis's students were articulating the continuum exemplar in all directions.

Another noteworthy feature of Curtis's presentation in St. Louis was that he made a parallel between the continuum model and explanatory devices recently developed in biosystematics:-

> "This variation commonly shows a continuous progression of changing combinations of both dominant and subordinate series, resulting in a vegetational continuum, rather than a series of separate, discrete and identifiable segments. The situation is comparable to the case in taxonomy when the breeding barriers between the two species break down. The resulting continuous variates may be studied but not classified."[179]

This was not simply a rhetorical connection. The leading bio-systematists Wendell Camp, whom we have seen also took an interest in Whittaker's work, and Edgar Anderson were frequent visitors to Madison.[180] They followed Curtis's work with great interest, as he did theirs. The two developments, both employing new methods in traditional fields, were parallel responses to the changed intellectual climate produced by the transformation of the life sciences by the development of genetics and the new Darwinian synthesis.

Acceptance of the individualistic hypothesis

Curtis proclaimed himself to be a disciple of Gleason:-

> "Throughout my phytosociological research I have constantly been stimulated by the ideas of H.A. Gleason, whom I consider to be the most outstanding plant ecologist of all time. He was so far ahead of his time that we have not yet caught up to him."[181]

He presented the Wisconsin work as a vindication of Gleason's early dissent from the community-unit theory. The continuum was the direct lineal descendant of the individualistic hypothesis. However, like Mason, Curtis felt it necessary to re-interpret and modify the individualistic hypothesis in the light of a new intellectual environment. In contemporary theories of plant behaviour, each species was precisely adapted to its own micro-environment or niche. Thus the role given to pure chance as an explanation for species distribution was diminished in Curtis's version of the individualistic hypothesis, as it had been in Mason's:-

> "I believe that the continuum concept to be only a slight modification of the individualistic concept,

in that it holds that species assemblages are formed by chance factors but that the innate adaptational behaviors of the available flora will imprint a pattern upon the results. All mixtures of species are not possible, only some of them."[182]

The individualistic hypothesis thus did not survive as a single unit-idea. It was altered as it was revived. The individualistic hypothesis showed the same essentially protean character as the community-unit theory it displaced. It was actively adapted and re-shaped by its utilisers in light of new problems and new circumstances.

By 1952, the Wisconsin work was beginning to attract widespread attention:-

"Our last paper on the northern continuum apparently was the straw that broke the camel's back. I am getting requests for all four papers at the rate of two or three a week from all corners of the world."[183]

It was discovered that similar work was being done in Australia and that the tropical ecologists were also beginning to doubt the validity of the association concept.[184] Follow-up studies had begun elsewhere in America. Stanley Cain wrote to Curtis:-

"This very pregnant idea [the continuum] is, as you know better than anyone else, stimulating lots of work. I expect a deluge of papers concerning it in the next few years. See what you've done."[185]

The exemplars offered by the continuum work were rapidly being adopted outside Wisconsin. There were still controversies to come, but Curtis was probably justified in his summing-up of the position of the competing theories in 1955:-

"Its current status seems to be a state of flux, with the great majority of investigators rapidly coming around to the Gleason individualistic hypothesis or a reasonable facsimile thereof. The last major holdout appears to be in the group of range managers in the Plains States who are still imbued with Clementsian doctrine."[186]

The authority of the Wisconsin school was enhanced by the increased mathematical sophistication of their approach to vegetation. From the mid-fifties, they began to employ techniques whereby stands were ordered not simply along a single continuum, but along several continua simultaneously. This technique, known as Multiple Ordination, was first devised in 1954 by Roger Bray, another of Curtis's students.[187] A further important landmark was the publication in 1959 of Curtis's large and impressive book The Vegetation of Wisconsin.[188] This encapsulated the results of the ten-year project begun in 1947. Based on many man-years of research by Curtis and his students, The Vegetation of Wisconsin was a regional study without rival in the United States.

Some indication of the success of the Wisconsin school is provided by the fact that three of Curtis's papers were among the 101 most highly cited botanical articles during the period from 1961 to 1972.[189] One of these highly cited papers was the original continuum paper by Curtis and McIntosh, and another was the original multiple ordination paper by Bray and Curtis.[190] None of Whittaker's papers appear on this list. So in 1959 Curtis was able to conclude:-

> " ... there is no longer any vocal opposition to the idea of a continuum by any responsible ecologist. It is an accepted approach and as such does not need to be continually tested or reproved."[191]

In fact, Curtis was being somewhat over-sanguine. Daubenmire, for instance, still had some vocal opposition to make.[192] But by the nineteen-seventies, it was true that no reputable ecologist in the English-speaking world worked routinely with the idea that vegetation occurred in distinct and definite associations.[193] Classification of vegetation was, of course, still a major research activity, but the units of classification were generally regarded not as natural kinds, but as instrumentally-useful categories.

Conclusions

In the introduction to the thesis, I pointed to the fact that science is an exclusive and hierarchical institution. I argued that the disciplinary history of ecology must take into account its position within the larger institution of science. The behaviour of ecologists has been shaped by the discipline's chronic problem of comparatively low status within the scientific community. We saw, in Chapter Two, how Clements sought to mimic the vocabulary and rhetoric of physiology in order to guide ecology toward scientific respectability. The present chapter presents many more examples of ecologists responding to an awareness that their practice was being found wanting in the light of the culturally accepted criteria of scientific knowledge.

We have seen how, in the new intellectual environment created by the success of the New Darwinian Synthesis, these problems were accentuated. American ecology's traditional practice seemed old-fashioned and unglamorous. Ecological research was unattractive to grant-giving bodies. The specialty's personnel was not increasing in number. Furthermore, ecology seemed unable to play a part in the harnessing of science to the national effort. This situation led certain ecologists to call for reform within the discipline to bring its practice into line with that of higher-status biological disciplines such as physiology and genetics.

Although the need for reform was widely accepted, the extent of the reforms advocated varied greatly. Daubenmire and Oosting advocated only mild innovations concentrated on introducing more quantification and experiment within the cognitive framework which they had inherited from their teacher, W.S. Cooper. They retained the community-unit as the primary object of inquiry. Mason, Cain and Egler, however, called for much more radical reforms and, in particular, the re-assessment of Gleason's individualistic hypothesis. I have argued that part of the attraction of the individualistic hypothesis was that it could readily be presented as being harmonious with the individual and population emphases of the New Darwinian Synthesis.

I also conjectured that the extent of reform which each actor advocated varied according to degrees of commitment to contemporary ecological practice. Daubenmire and Oosting, mainstream middle-status academics with relatively narrow ranges of expertise, advocated only mild reform.[194] Mason, Cain and Egler, with a wide range of skills and interests, were less attached to the old forms of practice and made sweeping condemnations of it. Even among these three, differences may be seen. Mason and Egler, one with his base in a different but related field, the other prepared to move out of ecology altogether, expressed their criticisms more strongly and were more radical in their proposals than was Cain.

What were required for successful reform were not polemics or prescriptions, but new exemplars - new models of ecological practice which were similar in form, at least apparently, to those of the higher status biological disciplines. This was what Whittaker and Curtis attempted to provide. I noted that it was still possible to do progressive work in the old ecological style and that neither Curtis's work nor Whittaker's provided a logical refutation of the older theories. In principle, the new work could have been accommodated within the older cognitive framework. But the social problems of the discipline were such that cognitive change was strategically advantageous.

In the reception afforded the work of Whittaker and Curtis, the hierarchical distribution of authority in science exercised its effects. Whittaker was first to invent new methods of investigation and to supply new data from which he argued not for the community-unit theory, but the individualistic hypothesis. However, it was the work of Curtis and his associates which was taken up by other ecologists and which led to the general revival of the individualistic hypothesis, or something very like it.

Whittaker was young, inexperienced and iconoclastic. He worked on his own. He had difficulty getting his work published. Experienced ecologists were able to cast aspersions on the scientific validity of his methods. Curtis, however, entered ecology trailing glory from his success as a physiologist. He saw the importance of devising new research techniques. He was well aware of what counted as scientific rigour and he was able to ensure that his work and the work of his students reached the appropriate standards. Avenues for publication were open to him. Curtis was, in many ways, a formidable opponent. His challenge to the ecological orthodoxy could not be contained as readily as Whittaker's.

A key feature of Curtis's success was his establishment of a productive team of investigators - the Wisconsin school as it came to be known.[195] The new techniques devised in Wisconsin were articulated rapidly in several directions at once. The total amount of new data, new methods and new practical models very quickly became impressive. The Wisconsin school were able to present a sustainable programme of research. New continua were discerned in a variety of vegetations. In all these ways, the status of the continuum as a fact in the world was greatly enhanced. Thus it was the Wisconsin work, and not Whittaker's, which provided the primary model for the next generation of studies using the individualistic hypothesis.[196]

However, this was not simply a story of the acceptance of an idea produced by Gleason forty years previously. The individualistic hypothesis was changed as it was adopted afresh. It was made harmonious with the theoretical framework which now dominated biological inquiry. The process of change and modification in response to new contexts which we traced throughout the history of the community-unit theory continued through its eclipse.

CONCLUSIONS

This chapter is in three parts. The first consists of the concluding remarks proper. The second section indicates, in more detail than has been possible in preceding chapters, how my interpretation of ecology's history differs from that contained in Ronald Tobey's recently published account of the Nebraska school. The third section returns briefly to the narrative to show that debates over the nature of vegetation did not die out in the nineteen-sixties.

Versatile and social historiography

The narrative has come a long way from Alexander von Humboldt, Naturphilosophie and the start of what Foucault terms the modern age. We have followed the history of vegetation science from its beginnings. We have traced its growth into a specialism in its own right. We have seen the rise of distinctive regional and national schools. In particular, we have followed the development of the idea that vegetation occurs in natural units - from its birth to its demise within one major national tradition of ecological inquiry.

The narrative has had sub-plots and divergences. However, I hope I have conveyed a sense of underlying unity. The thesis is intended to tell a single story - for the history of vegetation science is unified to the extent that new developments have continually been structured by past practice. I have described a continuous tradition of research, spanning more than a hundred and sixty years. Direct pupil to mentor links may be traced all the way from Robert Whittaker to Humboldtian plant geography. Similar connections may be found for the latest representatives of the European schools.

As well as displaying continuity, the development of vegetation science has been characterised by constant change and adaptation to new cultural circumstances. Continuity of tradition and contingency of response have been twin themes of my narrative.

It is worthwhile recollecting some of the other characteristics of the production of ecological knowledge which this study has highlighted. In the introduction to the thesis, I pointed to the need for historians of ecology to be eclectic in their choice of explanatory devices. History of ecology can neither be merely internalist, nor disciplinary, nor merely externalist, if it is to be faithful to its subject-matter. Ecologists display a wide variety of interests. Their commitments are located in many different aspects of the social structure.

At the internal level, we have seen the effect of purely technical interests such as those which Gleason and Braun-Blanquet displayed in applying floristic forms of analysis to the study of plant communities. I argued that such interests arose as a result of prior professional training. We have also seen the impact upon the development of ecology of technical developments such as sampling by quadrats and sampling by random pairs.

On the other hand, we have seen the importance of the larger social location of research activity. In Chapter Two, I indicated how botanists employed in the Land-Grant colleges needed to communicate with a lay constituency. This requirement was fulfilled in Clements's practice. This institutional situation also gave Clements the possibility of aspiring toward the role of ecological technocrat. The Sigmatists, in contrast, worked in an institutional context which supported pure research. The character of the ecological knowledge they produced was correspondingly different. My explanation of the contrast between the Sigmatists and the Clementsian ecologists was therefore largely in terms of the external relations of the institution of science as a whole. Chapter Two demonstrated how different external social situations played a part in producing different technical practices.

In our study of American ecology, we met another example of the importance of external relations. We saw the use of ecological knowledge in the wider sphere of political discourse. Arguments as to how society ought to be ordered were based upon what ecology had revealed nature to be. I argued that the existence of this usage led to particular forms of theorising being favoured by ecologists.

The internal and external relations already described do not exhaust the facets of ecology's social situation which must be taken into account if we are to have an adequate historical understanding of the construction of ecological knowledge. We must also consider the relations between ecology and the other sciences. We must consider the effect of factors external to ecology, but internal to science as a whole.

Vegetation science has always been a relatively low status discipline. Thus the accepted criteria of good scientific knowledge have always been framed not in ecology, but within other branches of science. Ecologists, therefore, have frequently had to modify their practice, or at least their rhetoric, to try to minimise the discrepancy between their cognitive standards and those of more prestigious disciplines. In Chapter Two, we saw how Clements adopted the vocabulary of physiology in response to such pressures. In Chapter Four, we saw how the reform of American plant ecology after the Second World War was mediated by the need to create a form of ecological practice which apparently coincided with culturally-given criteria of good scientific knowledge. Change took place to bring the theoretical apparatus of the discipline into line with those newly adopted by other higher status biological disciplines. Ecology thus presented a better image for peer scrutiny.

A somewhat different but related example of the effect upon vegetation science of its relation to other forms of knowledge production, is contained in Chapter One. There we saw how Alexander von Humboldt fashioned a study of vegetation according to the modes of aesthetic judgement and epistemological theory which prevailed in his cultural milieu. Drawing upon similar materials, I explained how vegetation came to be thought of as existing in natural units. At an even more fundamental level, we saw that a science of vegetation was only rendered possible by the widespread transformation of underlying cognitive assumptions which occurred at the end of the eighteenth century.

The thesis affords many other examples of the significance of the social location of ecological investigation. In the early years of vegetation science, Humboldt's maintenance of a network of scholarly patronage was a crucial factor in the successful development of vegetational plant geography. Even without an academic position, Humboldt was able to gather and inspire a loyal body of botanists who developed the exemplar of vegetation science contained in his published work. We have also seen how the shape of Gleason's career and, therefore, the degree of his involvement in ecological research, were determined by decisions he made as to which institutional position would offer him the best rewards in terms of remuneration, security, status, life-style and intellectual stimulation. We also saw the importance of the fact that Curtis was able to establish a considerable team of investigators in a secure institutional location with adequate financial backing. The existence of the Wisconsin school greatly aided the articulation, transmission, and acceptance of the new continuum exemplar.

These last three examples illustrate the crucial importance of social locations, for it is clear that the history of ecology would have been quite different if Humboldt and Curtis had not been able to maintain the collective research programmes they did. The history of ecology might well have been significantly different if Gleason had been able to find an institutional setting in ecology as rewarding as that he found as a taxonomist.

Any adequate history of ecology must, as I argued in the introduction, be internal history in that it must document the discipline's investigatory practice, its technical and cognitive developments, and its professional structure. But the historian of ecology must also consider that ecology, as a scientific discipline, is a dependent part of the institution of science as a whole, and that ecological thought has, throughout its history, intermeshed with social interests and intellectual trends of the widest possible provenance. I hope the above examples illustrate the range of explanations which the history of ecology demands. The need for such eclecticism renders any rigid distinction between external and internal influence on science artificial and meaningless. I have laboured throughout the thesis to display how natural knowledge is a part of culture. Culture is diverse but indivisible.

Saving the prairies - Ronald C. Tobey

The contents of this thesis are partly a development upon the work of those few other historians who have written on the history of ecology. I am greatly indebted to them all. Whenever I have been aware of a specific debt this has been acknowledged, and generally whenever I have noted an acute disagreement, this too has been pointed out.

One book deserves special mention in this context - Saving the Prairies by Ronald C. Tobey.[1] This is principally an account of, as Tobey puts it, the "life cycle of the founding school of American plant ecology". By the "founding school" Tobey means Bessey, Clements and the Nebraskans. Tobey's book is the only text whose coverage overlaps, to any appreciable extent, with the subject-matter of this thesis. I have learned much from it. I have also taken specific issue with Tobey at several points in the preceding chapters. I have commented, in Chapter One, on the lack of evidence for the split which Tobey makes between a mechanist and an idealist tradition in late nineteenth-century plant geography. I have noted, in Chapter Two, that, contra Tobey, there was little difference, as far as the context of ideological use was concerned, between organismic and mechanist metaphors of the plant community. I also have argued that Tobey's treatment of the ideological basis of Clements's organicism is seriously incomplete. However, for the most part, the interpretation of the history of ecology that Professor Tobey expounds is so radically different from my own that it is difficult to engage with him at specific points. If I had tried, my chapters on Clements and Gleason would have been occupied with little else. Instead I will indicate here where the principal differences lie.

Tobey attempts to trace the development of the Nebraska or 'grassland school' of plant ecology on the basis of a specially-prepared bibliography. He made as full a list as possible of all the articles or books which were listed or indexed in Botanical or Biological Abstracts, between 1918 and 1955, under the subject headings 'ecology' or 'grassland' and which dealt with the mid-western United States. Titles for the period before 1918 were taken from standard textbooks such as Weaver and Alberton's Grasslands of the Great Plains. When graphed, the number of publications per year follows what Tobey has called the

'Kuhn-Crane' curve. That is to say, frequency of publication starts slowly, rises quickly after 1916, levels off, and then falls. Tobey regards this curve as representing the life-cycle of the Nebraska school as it passed from the pre-paradigm stage, through normal science to a period in which it had solved its major problems and in which anomalies began to accumulate. Eventually, paradigm 'exhaustion' and crisis ensued.

As well as charting the progress of the Nebraska school, the bibliography allows Tobey to draw more general conclusions about the development of plant ecology in America. Thus from his list of titles he concludes that the Chicago school declined earlier than the Nebraskan:-

> "Earlier they [the Nebraskans] had been a group of scientists offering a microparadigm in competition with an alternative microparadigm from Chicago; by the 1930s, they were the establishment, the competitors having withdrawn."[2]

But the grassland bibliography, or indeed any bibliography, is too narrow a base to support such judgement. As we have seen, in the nineteen thirties, W.S. Cooper was training men who were to be leaders of the next generation of plant ecologists - Oosting, Daubenmire, Egler and Murray Buell.[3] Cooper, although in Minnesota, had been a student of Cowles and was as much a Chicagoan as Clements was a Nebraskan. At roughly the same time, Stanley Cain was in Chicago, studying under Cowles.[4] The Chicago school was far from defunct. As late as the fifties and sixties, botanical presidents of the Ecological Society of America were still regularly students, or students of students, of Cowles.[5] Chicagoan ecology was evidently alive and well long after Tobey's bibliography declares it dead.

There are two possible, perhaps complementary, explanations for Tobey's misconceptions. One is that the Chicagoans such as Cowles, Cooper and Fuller published less than the Nebraskans, but what they did publish was, per unit, relatively more important. This seems likely since Tobey's bibliography includes a large number of the semipopular monographs of the agricultural experiment stations and the publications of the United States Department of

Agriculture.[6] These titles would contain much educational and advisory material. The purer, less applied, emphasis of science at the University of Chicago would lead to fewer publications of this nature. One would expect the Chicagoan literature to be less voluminous, containing little else but the products of original research. However, it would be addressed solely to an audience of researchers rather than partly a wider lay constituency. Therefore it would be, per unit, more likely to stimulate further ecological research. Furthermore, Tobey's concentration on published material inevitably diminishes Cooper's and Cowles's historical importance as teachers.[7]

The second possible explanation is that Tobey's key-word criteria miss some important papers. It seems likely that his concentration on 'grassland' as a key-word would favour the Nebraska school. Cowles, Cooper and their students principally studied woodland vegetation and its development. Perhaps Tobey ought to have included 'forest' in his list of key-words. But, as is obvious from my bibliography, even under such extended criteria, many of Gleason's, or even Cooper's, papers would not have qualified. One is forced to the conclusion that historical judgements are better based on the analysis of content and context than upon citations and key-words.

Throughout his book, Tobey exaggerates the importance of Clements. In Tobey's account Clements appears as a Colossus astride American plant ecology. Tobey mentions no American critic of Clements other than Gleason. But, in the preceding chapters I have frequently pointed out that, despite his undoubted influence, Clements's positions on many matters were generally regarded as extreme. I have provided evidence that Clements was isolated from the majority of American ecologists. Tobey misses the broad spectrum of opinion which existed between Clements and Gleason.

One reason for Tobey's over-estimation of Clements is that he routinely takes Clements's rhetoric as an accurate description of his actual practice. To Tobey, therefore, Clements achieved the quantification of ecology:-

> "The invention of a quantitative method for ecology was more than the clever application of statistics.

> The invention of the quadrat, or meter-plot, embodied a profound epistemological shift, in which the scientists ceased to believe in the reality of one phenomenon and began to believe in the reality of another phenomenon. Ecology had "taken leave of its senses", and hitched its intellect to mathematics. It was a shift analogous to the shift in astronomy from the Ptolemaic earth-centered observational astronomy, or the shift from Aristotelian physics based on the phenomenal qualities of motion to the Galilean physics of hidden mathematical laws that lay, as reality, behind the phenomena."[8]

This is a startling claim and, it seems to me, a false one. One is tempted to reply 'What statistics? What mathematics?' An inspection of Clements's published work shows that even after the invention of the quadrat, his methods remained essentially descriptive and observational. Plant Succession, which Tobey regards as the paradigmatic book of the Nebraska school, contains little statistical, mathematical or quantitative work, other than the simple enumeration of species. Tobey claims that Clements believed that his German inspirer, Drude, had made a fundamental methodological error in demarcating the boundaries of the North American prairie without counting quadrats in it. But Clements and his associates frequently made similarly non-quantitative demarcations. Clements's characterisation of the Lake Forest was controversial partly for this reason. There is no doubt that Clements did advocate increased quantification and experiment. However, I have interpreted this advocacy as a tactical manoeuvre designed to raise the prestige of ecology by identifying it more closely with physiology.

Even if we accepted that Clements did produce a profound epistemological shift comparable with Galileo's, it would be difficult to accept Tobey's characterisation of it. Tobey argues that the shift was away from typological thinking. According to Tobey, Darwin had "destroyed the sensory typology that had underlain classification in biology".[9] Species were no longer considered to be defined by an inherent essential principle. In nature, all was flux.

Tobey argued that Clements, influenced by the widespread adoption of Darwinian modes of thought, extended this destruction to ecology. Leaving aside Clements's opposition to the Darwinians on the species question, we may note that the entire thrust of Clements's theorising was that vegetation-units did exist in nature. They were not classifier's categories. There was nothing arbitrary about them. They were natural kinds of vegetation. I have shown that this was certainly how Clements's work was perceived by his peers.

Furthermore, Clements defined and identified these vegetation-units according to physiognomy. Each formation had a distinctive physiognomy which was the expression of the prevailing climate. Thus, contrary to Tobey's argument, Clements demarcated vegetation-units according to a typology of plant form. This was a typology perceivable directly by sense impression. Furthermore, it was also an ideal typology since the formations were held to be potentially rather than actually in existence throughout the entire area of each climatic region. Thus it is difficult to credit Clements with a determined departure from essentialist or typological thinking.[10]

Tobey places great importance, in this context, on Pound and Clements's demonstration that it was difficult to delimit the boundary between the prairie grass association and the buffalo grass association.[11] However, it is clear from Clements's later work that he considered this difficulty existed partly because the real biological boundaries lay elsewhere. The real unit, the vegetation-organism, was not the individual association but the grassland formation as a whole. Clements did not deny the existence of real boundaries; he merely relocated them.

As part of his attempt to make Clements out to be a nominalist Darwinian, Tobey frequently argues that Clements worked with a notion that vegetation varied continuously. To an extent this is true. Clements did acknowledge that no two pieces of vegetation were identical. He pointed out that seres and ecotones often exhibited gradual change.[12] But Tobey takes Clements's statements on continuous variation out of their historical context and changes their significance. We have seen that Clements's remarks on vegetational variation were not regarded, by his peers and immediate successors, as the central tenet of his description of vegetation.

To his contemporaries, Clements's work was predicated upon the assumption that there were definite units of vegetation. The units were the primary reality, despite the existence of much variation. Vegetational boundaries might be blurred, transitions gradual, but the monoclimax hypothesis and the requirement of uniform physiognomy both entailed that each formation was a fundamentally different kind of vegetation from the next. That was the Clementsian tenet that Gleason chose to dispute.

As he exaggerates the importance of Clements, Tobey fails to give Cowles his full significance. I have shown how Cowles's clever harmonising of the German system of vegetation classification with peneplain geology provided American ecologists with an important new theoretical principle and a powerful organising device. Tobey, however, writes that compared to the Nebraskan invention of the quadrat:-

> "Scientists at the University of Chicago did not have innovations of a similarly original character"[13]

This is to underestimate the importance of physiographic ecology. In Chapter Three, I described how widely influential Cowles's innovations were - on Clements amongst many others.

Tobey's programmatic pronouncements in the introduction to his book are very attractive:-

> "Establishment of scientific ideas here appears less as the victory of truth over error than the building of networks of collaboration, placement of graduate students in strategic jobs, and who cites whom."[14]

But, just as he fails to extend his social and ideological analysis to the genesis of scientific knowledge, so he does not consistently eschew truthfulness as an explanation for an idea's popularity, nor error as an explanation for its failure. He is continually getting tangled up in ahistorical questions of logic and meaning. Tobey refers to Gleason in a manner which, given his programmatic statements, is somewhat judgemental:-

> "In Gleason's universe ... there were only individual organisms ... This position was philosophically untenable, as any nineteenth century idealistic philosopher would quickly have shown, but Gleason ... whistled his tune, oblivious to the cemetery of

buried doctrines similar to his ... Gleason did not recognise the ontological problem with his concept of species."[15]

Tobey's interpretation of the Clements/Gleason dispute seems to be that Gleason held the individualistic hypothesis because he simple-mindedly did not comprehend the rich complexity of the Clementsian system:-

"Clements's critic, Henry Gleason, did not understand that Clements held concepts both of continuity of vegetation and of naturally limited organic boundaries ... He did not understand that Clements accepted the continuum concept in analyzing the spatial arrangement of the ecotone and even the interior of the association."[16]

I hope I have indicated that it is possible to achieve a fuller understanding of Gleason's attitude than this. Both Gleason and Clements accepted that vegetation varied even within associations. They differed as to the consequences to be drawn from the existence of this variation.

Tobey and I agree that important changes occurred within the discipline of ecology in the nineteen-fifties. However, he argues that these were endogenous, being due to the Clementsian paradigm becoming exhausted. This seems dubious on theoretical grounds, since it suggests that the capacity of any paradigm is finite. The social nature of knowledge production would seem to imply the opposite. In principle any research programme is infinitely extendable and infinitely flexible. Furthermore, the work that Daubenmire, for example, produced in the fifties, shows that, in fact, it was still possible to produce good work within the old ecological style. In Chapter Four, I have argued, contra Tobey, that the pre-Second World War paradigm did not fall. It was pushed. It was abandoned as a result of strategic decisions made because ecologists required, for institutional reasons, new forms of theory and practice.

The above are a selection of the historical and methodological points on which I differ from Tobey. Overall, I hope that my thesis fulfils Tobey's programme rather better than Saving the Prairies does.

Coda - the debate goes ever on

I would not like to leave the impression that the revival of the individualistic hypothesis silenced debates over the character of vegetation. This was not the case, even in America. As we have seen, this debate was only partly a technical one. It also involved wider social issues. One might conjecture that for as long as scientific ideas of nature are invoked in this external social context, controversies as to how nature is best conceived will continue. Certainly the debate as to the nature of vegetation has continued in both American and British ecology until the present day. As a coda to the thesis, I will briefly describe these sustained differences of opinion about the natural world.

In Chapter Four, I documented changes which occurred in the theory and practice of plant ecology in the nineteen-fifties. But larger changes also took place in the discipline of ecology as a whole. The older descriptive study of plant communities was rendered obsolete not only by continuum theory and gradient analysis, but also by a new emphasis on the ecosystem as an object of study. The ecosystem theorists considered plants, animals and the relevant aspects of the inanimate habitat all together in a study of functioning relationships.

The 'New Ecology', as it was called, was distinguished from the old not only by its new object of study, but also by a concentration on the monitoring of energy and nutrient flow between the various biotic elements of the ecosystem.[17] Vegetation science did not decline in importance, but ecosystem studies became the most prestigious branch of modern ecology. The New Ecology was a quantitative mode of research, often involving much instrumentation, and leaning, at least in principle, upon the mathematics of systems theory.[18] It lent itself to pursuance in team projects. With the New Ecology, ecology became 'Big Science'.[19] It was, all in all, a form of study eminently suited to coincide with widespread contemporary criteria of what science ought to be.[20]

The relevance of this development to our present concerns is that many New Ecologists wrote about ecosystems in terms strikingly similar to those in which Clements had described his units, the formations or biomes.[21] The vocabulary was changed, the location of the natural properties was different, but the meaning was the same. The ecosystem was presented as possessing an holistic unity, as greater than the sum of its parts. As Eugene Odum put it:-

> " ... unique principles ... emerge at the supra-individual levels of organisation."[22]

The entire ecosystem was held to constitute a single natural entity. Adjustment to the environment took place at the level of the ecosystem as a whole, not solely at the level of the individual, or the species, or the population:-

> "We theorized that new sytems properties emerge in the course of ecological development, and that it is these properties that largely account for the species and growth form changes that occur ... [T]here is a holistic strategy for ecosystem development."[23]

Mature ecosystems were climax communities which maximised biological productivity.[24] The development of ecosystems was necessarily directional - from the simple to the complex, toward maximal productivity. Mature ecosystems were also characterised by homeostatic community mechanisms which maintained a steady-state:-

> "Where all the components of a community turn over several times a year there would be ample opportunity for changes to occur if there was no self regulative mechanism."[25]

Such pronouncements by New Ecologists such as the brothers Howard T. and Eugene P. Odum did not, however, meet with universal approval. Not everyone saw the attractions of holism, in its new or its old guise. John T. Curtis, champion of the individualistic hypothesis, for example, reacted strongly against the Odum approach:-

> "Only by getting many people to see the weakness of the Odum techniques will this evangelistic school be restrained ... He [H.T. Odum] should clarify his use of "tropical rain forest". Now that Beard and Richards have cleared up the matter there is no excuse to let a mere zoologist throw us back into chaos again. Also omit or document the assertions about steady state, climax, etc. Also modify and correct the sections on species diversity.
>
> The style is annoying, rather like brother Gene. Both behave like old-fashioned school-masters, setting the ignorant readers straight on the basic issues by means of dogmatic unfounded dicta."[26]

The Odums were indeed to prove ecological evangelists. Eugene Odum has become one of the most vocal public proponents of scientific ecology.[27] And, like Clements, in his appeal to a wider audience, he has repeatedly drawn morals for human society from the holistic properties of natural ecosystems. As nature is holistic and mutualist, so should be man's relationship with his fellows and with the natural world:-

> "Do these coral reef discoveries have any significance for urban industrial man? Perhaps they do. The Pacific coral reef, as a kind of oasis in a desert, can stand as an object lesson for man who must now learn that mutualism between autrophic and heterotrophic components, and producers and consumers in the societal realm, coupled with efficient recycling of materials and use of energy, are the keys to maintaining prosperity in a world of limited resources."[28]

Political policies designed along ecological lines, utilising the expertise of ecologists, would lead to a reduction in waste and an increase in social harmony:-

> "Since the kind of sectional conflicts which for so long hampered our national development are now appearing on a truly frightening scale in the confrontations between so-called "advanced" and "backward" nations, even a partial success at coastal zone management would have a favourable global impact by demonstrating that action based on holistic values and properties is a viable alternative to development on the basis of competitive exclusion alone."[29]

Eugene Odum thus allied himself to an ecological ideology which attracted many adherents in the nineteen-seventies. As Lowe and Warboys put it:-

> "The appeal to ecology has gone beyond the search for tactical responses and technical solutions to particular environmental problems, toward the claim that ecology can contribute to a radical reordering of human purposes ... "[30]

The image of a harmonious natural order was a virtually universal feature of this rhetoric. The desirability of an orderly efficient human society was deduced from an orderly efficient nature. Odum is thus quite typical in legitimating his social prescriptions with technical arguments as to the observable characteristics of ecosystems.

But not all ecologists agree that nature is holistic and mutualist. Many follow Curtis and prefer to regard vegetation in individualistic terms.[31] Professor John Harper, for example, has vigorously expressed his dissent from the maximal productivity and mutual aid school. In doing so, he employs vivid and evocative social imagery:-

> "A theory of natural selection that is based on the fitness of individuals leaves little room for the evolution of populations or species toward some optimum, such as better use of environmental resources, higher productivity per area of land, more stable ecosystems or even for the view that plants in some way become more efficient than their ancestors. Instead, both the study of evolutionary processes and the natural behaviour of populations suggest that the principles of "beggar my neighbour" and "I'm all right, Jack" dominate all and every aspect of evolution ... Natural selection is about individuals and it would be surprizing if that behaviour that favoured one individual against another was also the behaviour that maximised the performance of the population as a whole."[32]

We can see that the controversy between Odum and Harper has the same pattern as that between Clements and Gleason, one stresses the integrity of holistic collective entities, the other regards the individual as the only viable level of explanation. Further research would be required to characterise the Odum/Harper controversy fully. My conjecture that it has a social basis is simply a conjecture. However, the point I wish to make in this coda is that the new data, new modes of research, new theories, which emerged in the fifties, did not conclusively and unequivocably elucidate the nature of vegetation. One seeks in vain for a theoretical or empirical resolution of the Clements/Gleason debate. It flows on, taking new expressions and no nearer conclusion than ever. As I hope this thesis has shown, the roots of controversy about Nature often lie too deep in the social fabric for scientific observation, experiment or theory ever to wither them away.

NOTE ON SOURCES

As already mentioned in the Acknowledgements, in the course of preparing this thesis I consulted the following archival collections:- The Henry Allan Gleason Papers held in the Library of the New York Botanical Garden, Arthur G. Tansley's correspondence held in the care of Professor West, Department of Botany, University of Cambridge, and the John T. Curtis Papers held in the Archive Division, University Library, University of Wisconsin, Madison. In the following notes, these sources will be referred to as Gleason Papers, Tansley Papers, and Curtis Papers, respectively.

The Gleason archive consists almost entirely of correspondence. The letters are well-organised in boxes, by year, and within each year alphabetically by the name of the correspondent. There is no index but individual letters are easy to find and I have not considered it necessary to give details of box location. I have photocopies of many of the items to which I refer. The New York Botanical Garden also holds some unpublished Gleason material other than correspondence - mostly typescripts of unpublished articles, together with a short memoir. These items are bound and entered in the Library's main catalogue. Details of these items, if utilised, are given in my main bibliography.

The Curtis archive consists principally of twelve boxes of correspondence, with some personal notes. Again it is well-organised chronologically and alphabetically, and I have not specified box location. I have photocopies of many of the items to which I refer. The archive also contains six further boxes of material other than correspondence - mainly unpublished lectures and reports. These are arranged alphabetically by title.

The Tansley archive consists of three boxes of miscellaneous material - letters, draft articles, a travel diary - found by Sir Harry Godwin among the volumes of Tansley's library. The material is not organised in any way, but the amount of correspondence is quite small and particular letters ought to be easy to locate. I have given the box location of each item I have referred to.

I have also taken much material from my recorded conversations with botanists and members of Gleason's family. I will refer to these conversations in the following manner, viz., Interview, F.E. Egler. The date and place of each interview is given in the Acknowledgements. Several of these tapes have been wholly or partly transcribed and the transcripts are available for inspection on request.

N O T E S

INTRODUCTION

1. Perhaps here I should have written "what is held to be ecological knowledge". I do not mean to imply that ecologists actually make decisions on these or any other political matters. For ecologists' entanglements with decision-making, see Nelkin (1977) and Lowe (1975).

2. Worster (1977), p.vii.

3. Recent important contributions to the history of ecology have been: Tobey (1981), Cittadino (1981), and Kingsland (1981).

4. McIntosh (1976) and Egerton (1977) give a good impression of the historical importance of plant studies within ecology as a whole. Mills (1969) illustrates the importance of the community concept in another branch of ecology - marine benthic ecology.

5. My usage here is the same as that of Lowe and Warboys (1980).

6. For examples of good 'internal' history of the type referred to here, see Pickering (1981) or Dean (1979).

7. For a good description of the competitive and hierarchical nature of modern science, see Hagstrom (1965), especially Chaps. 2 and 4. See also Mulkay (1977).

8. Ecology's low status and its consequent problems are discussed in McIntosh (1980), p.219.

9. For a discussion of the recent recognition that it is not easy to disengage internal from external questions, see Macleod (1977).

10. The term 'actor' is used throughout in its technical sociological sense, see, for example, Goffman (1956). The best articulated and most cogent account of the theory of social interests and its use in historical explanation is to be found in Mackenzie (1981), pp.216-225 _et passim_. Unlike Mackenzie, however, I am not afraid to ascribe interests to individuals as well as to the social structure.

11. For reasons of clarity of exposition, I will however adopt a somewhat different vocabulary when referring to interests situated in the internal rather than the external context, see footnote 15 below.

12. See, for example, Chisholm (1973).

13. What is referred to here is the existence within ecology of a 'knowledge constitutive interest' in prediction and technical control as proposed by Habermas (1972), p.308. But, see also Barnes (1977), Chap. 1, and Mackenzie (1981), pp.210-216.

14. Douglas (1972).

15. For a recent discussion and literature review of the moral use of ideas of nature, see Shapin (1982).

16. For sociological perspectives on this current activity, see Cotgrove (1975) and Lowe and Warboys (1980). The works cited in the reference lists of both papers afford many examples of explicit sermonising. See also Colwell (1970).

17. I have already mentioned the theory of social interests, see footnote 7 above. Roughly speaking, I will use the term 'social interest' to refer to actors' commitments to actual or desired features of the structure of society in the widest, the 'external', sense. The term 'cognitive interest' seems to have recently fallen out of favour among sociologists of science, but I will employ it here since it seems to serve my purpose well enough. What I mean by 'cognitive interest' is a commitment to a particular feature of scientific or intellectual practice, such as a commitment to a particular methodology, a particular mode of theorising or a specific body of technical resources. That is to say, a cognitive interest differs, in my usage, from a social interest in that the former term refers to a commitment to an aspect of the internal social structure of a cognitive activity rather than referring, as the latter term does, to a commitment situated within the external social environment. Both social and cognitive interests may, however, be involved in the construction of technical knowledge. To take examples from the following chapters, Gleason's interest in a floristic approach to vegetation would be regarded as 'cognitive'; Clements's interest in establishing an environmental technocracy would be regarded as 'social'. The distinction is, of course, to a large extent a vague and arbitrary one. But it is one that I have found to be useful in organising the present study. For examples of the usage of the term 'cognitive interest' in approximately the sense it is employed here, see Mackenzie (1978) and Pickering (1980).

18. For references to works by Foucault, see Chapter 1 below.

19. For a glimpse of the many research schools and traditions that have been omitted from this thesis, and the complexity and scope of twentieth-century plant ecology, see Whittaker (1962).

20. Nor are scientific controversies the heroes of the tale. Despite the fact that the difference of opinion between Clements and Gleason over the nature of the plant community dominates a large part of its text, the thesis is not meant as a contribution to the literature on scientific controversies and should not be

read as such. The mechanics of the quarrel between Clements and Gleason are only of secondary interest. My principal concern lies with how, due to a complex of skills, prior training and social interests, different practices diverged from a common tradition. In the elucidation of this process, the Humboldtians and the Sigmatists are as important as Clements and Gleason, although I do not describe in detail any controversies in which the former two were engaged.

21. The distinction being made here is the same as that made between the 'contemplative' and the 'social' conceptions of the nature of knowledge by Barnes (1977). The penultimate sentence of the paragraph is virtually a paraphrase of one of Barnes's (p.2).

22. I have discussed elsewhere the pitfalls of assuming disciplinary continuity between one historical period and the next (Nicolson, 1982).

23. See Bloor (1976) and Barnes (1974). Whether either of these authors would accept my efforts as exemplifying the 'strong programme' is another matter. Other presentations of the relativist-constructivist approach include Collins (1981) and Knorr (1981).

24. The most sophisticated statement of the view that history is essentially a narrative form is to be found in Ricoeur (1979). See also W.B. Gallie (1964).

25. Note however that my argument here should not be construed as implying that there is any fundamental difference in kind between the historical and the sociological, or for that matter the scientific, understanding.

26. Whittaker (1962), p.123.

CHAPTER 1

1. For remarks along similar lines, see McIntosh (1958) p.115, and Ashby (1936), pp.221-2.

2. See Egler (1977) p.8 for a further elucidation of the distinction between flora and vegetation.

3. Green (1914) pp.229-91 remains a good description of the taxonomic interests of eighteenth-century botanists. See also Allen (1976) pp.26-51 and Stafleu (1971a).

4. Humboldt (1807b) p.7. See also Brewer (1960) p.2.

5. Linnaeus (1751) pp.263-270.

6. See Du Rietz (1957) pp.161-68.

7. Moss (1910) p.27.

8. For an elucidation of the "Economy of Nature" concept as it is relevant to the present discussion, see Limoges (1971) and (1972). See also Worster (1977) pp.1-55, and, for more general background, Glacken (1973) pp.501-50.

9. See Linnaeus's "The Swedish Pan" and "The Oeconomy of Nature", English translations in Stillingfleet (1762).

10. Egerton (1973) pp.335-7, Worster (1977) pp.31-55.

11. I have argued this in detail elsewhere (Nicolson 1982). The principal point to be made is that, while men in the eighteenth century certainly studied the interrelations between Man and Nature, and between species within Nature, these investigations were maintained by quite a different cognitive framework from that which pertained in the nineteenth century - namely physico-theology.

12. Humboldt (1821-25) p.iii.

13. Nordenskiold (1928) pp.560-61; Raup (1942) pp.319-25.

14. Grisebach for example published The Flora of the British West Indian Islands (1859-64) as well as Die Vegetation der Erde nach ihrer klimatischen Anordnung (1872).

15. See Whittaker (1962) p.4.

16. For a general assessment of the inadequacy of the classic language of discovery, see Kuhn (1962) pp.52-65, also Barnes (1982) pp.41-45, and Brannigan (1981).

17. Pickering (forthcoming, b).

18. For a version of the case against the existence of an independent observation language, see Hesse (1974). For a discussion of empirical demonstrations of this point of view, see Shapin (1982) pp.2-8.

19. Nicolson (1982).

20. For further elucidation of the notion "producing a world", see Pickering (forthcoming, a).

21. That the classification of vegetation into types is a relativistic and instrumental exercise is argued by Whittaker (1956) pp.40-43. For the more general argument that all classification has this nature, see Barnes (1981) and Bloor (1982).

22. For an exposition of the view that this is a good stance for those who study science to adopt, see Bloor (1976).

23. This change is well characterised in Foucault (1970) - see, in particular, chap. 5.

24. Ibid. p.132. Foucault's views on classification in the eighteenth century have been elucidated by Pratt (1977).

25. Ibid. pp.132-38.

26. Linnaeus (1735). I have quoted from the English translation of Engel-Lebeboer and Engel (1964) p.19.

27. Ibid.

28. Foucault (1970) pp.46-124.

29. Ibid. p.162; also Hartshorne (1939) p.44. Foucault uses the term episteme to refer to the totality of assumption upon which discourse is based, in any given historical period. His use of this term has been elucidated by Sheridan (1980).

30. Kant's lectures on physical geography are contained in Kant (1902-1966) 10, pp.151-436. His introduction has been translated into English by May (1970) pp.255-64.

31. May (1970) p.259. See also Hartshorne (1939).

32. May (1970) p.260.

33. See Bowen (1981) pp.206-9.

34. Quoted in Hartshorne (1939) p.44. See also Hartshorne (1958).

35. Quoted in Hartshorne (1939) p.44.

36. Ibid.

37. Quoted in ibid.

38. Ibid.

39. Ibid. p.45. See also Huggins (1935).

40. Macpherson (1972) p.23.

41. Browne (forthcoming) pp. 31-38. Page numbers refer to a pre-publication typescript. I am greatly indebted to Dr. Janet Browne for very kindly allowing me to consult her book before its publication. This has immensely improved my understanding of early plant geography. I hope that the present chapter will complement Dr. Browne's work. She describes the development of floristic plant geography; I describe the tradition of vegetational plant geography.

    It should be noted, however, that Dr. Browne's concern, in the latter portion of her book, is principally with developments made by English-speaking investigators. She mentions no continental European geographer after Alphonse de Candolle. The insularity of British plant geography after 1840 has been described by Nelson (1978). Nelson is however unable to specify what precisely British plant geography is isolated from. I would suggest it was isolated from Hamboldtian plant geography.

42. Browne (forthcoming) pp. 59-64.

43. Ibid. p.36.

44. The most complete source for J.R. Forster is Hoare (1976).

45. Forster (1778) p.215.

46. Ibid. p.176.

47. Ibid. p.174. See also Browne (forthcoming) p.41.

48. Browne (forthcoming) p.43.

49. Forster (1778) p.174.

50. Ibid. p.176.

51. See Glacken (1973) p.613.

52. Browne (forthcoming) p.44.

53. Forster (1778) p.174.

54. See Browne (forthcoming) Chap. 2.

55. For biographical details of Willdenow, see Bylebyl (1975) and Konig (1893) pp.95-98.

56. Willdenow (1792). I have quoted from both the first (1805) and the second (1811) English editions.

57. Bylebyl (1975) p.386.

58. Willdenow (1811). The section on terminology occupies pp.13-151 of the second English edition.

59. *Ibid.* p.136.

60. *Ibid.* pp.3-4.

61. *Ibid.* pp.152-85.

62. Hoare (1976) p.22.

63. Willdenow (1805) p.337.

64. Willdenow (1811) pp.415-6.

65. Willdenow (1805) pp.393-4.

66. *Ibid.*

67. For a good account of Willdenow as a floristic plant geographer, see Browne (forthcoming) pp.45-9.

68. Willdenow (1805) p.378.

69. *Ibid.* p.402.

70. Hein (1959), see also Konig (1893) especially pp.80-81, 117-124.

71. Meyer-Abich (1969) p.20.

72. Browne (forthcoming) p.46.

73. The best account in English of Humboldt's life and work remains Lassel's two-volume translation of Bruhns (ed.) *Life of Humboldt* (1873). See also Botting (1973). The best German biography of Humboldt is Beck (1959-61).

74. For a good characterisation of "physique generale" see Cannon (1978) pp.73-79. For an excellent discussion of the aims of Humboldt's universal science, in particular, its relationship to *Naturphilosophie* and empiricism, see Bowen (1970).

75. Bowen (1981) pp.211-2.

76. Bruhns (1873) *1*, p.86.

77. Humboldt (1793) pp.9-10, trans. Hartshorne (1958) p.100.

78. Beck, the author of the most recent full-scale biography of Humboldt, described the *Flora Fribergenis Specimen* in the following terms:-

"Wie Kant, un geistgeschichtlich im Zusammerenhang mit ihn, entwickelte Humboldt eine Gliederung der Geographie, die er bis an seim Lebensende beibehielt. Die erscheinungen Können nach drie Gesichtspunkten behandelt werden: dinglich-systematisch, historisch und chronologisch." Beck (1973) 1, p.60. Quoted by Tobey (1981) p.92.

79. See Coleman (1977) pp.1-8, for a description of this transformation.

80. Albury and Oldroyd (1977).

81. *Ibid*. p.203 (my emphasis)

82. *Ibid*. p.202.

83. Humboldt (1793), trans. Hartshorne (1958), p.100.

84. For Göttingen, see Lenoir (1981). The best sources for the research activity of Muséum d'Histoire Naturelle are works on Lamarck; see Schiller (1971) and Stafleu (1971). For the institutional background, see Limoges (1980).

85. Humboldt (1807a).

86. Bruhns (1873) 1, pp.83-87.

87. Forster (1777).

88. Botting (1973) p.21.

89. Bruhns (1873) 1, pp.373-90.

90. For the importance Humboldt attached to his experience of the tropics, see Humboldt (1849) p.215.

91. See Botting (1973) p.213.

92. Forster, G. (1791).

93. Meyer-Abich (1969) p.101.

94. This point is made by Meyer-Abich, *op.cit*.

95. Humboldt (1807a) p.VII.

96. *Ibid*. pp. V-VI.

97. Humboldt (1850) p.214. The *Ideen zu einer Physiognomik der Gewächse* was first published in *Ansichten der Nature* (1808) which was later translated into English, Humboldt (1850). All references to the *Ideen* are taken from the Bohn's English translation of the third edition of the *Ansichten*.

98. Humboldt (1807a), p.42. I am aware that the exact meaning of the first sentence of this quotation is difficult to discern. However, I believe the meaning of the paragraph as a whole is quite clear.

99. See Smith (1960), Chapter 1 and pp.64-65.

100. Humboldt (1807a), pp.30-31.

101. Humboldt (1850), p.217.

102. Humboldt (1807a), p.1.

103. Ibid., between the preface and the main text. The engraving is not to be confused with the "Tableau Physique des Regions Equinoctiales" which is a collection of physical and phytogeographical data, bound in the same volume as a supplement to the Essai, Humboldt (1807a), pp.37-152. The engraving and the physical tables relate to the same region, however, and the former may be taken to be the graphical representation of the latter.

104. Bruhns (1873), 1, p.179.

105. Humboldt (1795).

106. Bruhns (1873) 1, pp.161-78.

107. Humboldt (1807b).

108. For a description of Goethe's botany, see Arber (1950), Chaps. 4 and 5.

109. Bruhns (1873) 1, p.176.

110. The text of Schiller's letter to Körner 6th Aug. 1797 on the subject of Alexander von Humboldt is quoted in Bruhns (1873) 1, p.188.

111. Ibid. p.172. Goethe was vehemently opposed to the vulcanist theory of the creation of the Earth's crust, a theory Humboldt adopted upon his return from America.

112. Humboldt (1808), see note 97 above. Humboldt's comments on the Ansichten der Nature are quoted in Bruhns (1873) 1, p.357.

113. Humboldt (1844) - I have used the English translation (1846-58) - see, for example, 2, pp.6-7.

114. See, for example, Ibid. 1, p.37.

115. Letter to Varnhagen, April 28th 1841, Humboldt (1860) pp.67-68.

116. In particular, Von Engelhart (1976). Lenoir (1981) provides a guide into this literature. Von Engelhart has identified three distinctive traditions within Naturphilosophie; the "transcendental" which he identified with Kant and which Lenoir associates with Blumenbach and the Göttingen school, the "speculative" or "romantic" which he identifies with Schelling, and the "metaphysical" which he identifies with Hegel and within which Lenoir places the biological work of Oken, Goethe and Carus.

117. Humboldt (1850), p.219.

118. Ibid. pp.229-230. Humboldt, although closely associated with Blumenbach, must be, therefore, seen as electic even within Naturphilosophie.

119. Bruhns (1873) 1, p.188 - see note 110 above.

120. Mannheim (1952), pp.79-94.

121. Ibid. Chap. 2.

122. The most detailed study of Humboldt's political views is Braun (1954a). See also Bruhns (1873) 2, pp.242-55 and Rippy and Braun (1947). For the difficulties Humboldt's liberalism caused him in Prussia, see Kellner (1963) p.218.

123. See Lenoir (1980).

124. Jordanova (1976), Chap. 3.

125. Lenoir (1980).

126. See Gillispie (1962).

127. Lenoir (1981).

128. See Bowen (1970) and Kellner's description of Humboldt's lectures on physical geography, Kellner (1963), p.115.

129. Lenoir (1981).

130. Bruhns (1873) 1, p.69.

131. Ibid. 1, p.83.

132. Ibid. 1, p.72.

133. Lenoir (1981), pp.170-4.

134. Ibid. p.170.

135. For a lengthy discussion of the links between Humboldt and Kant, see Macpherson (1972) pp.34-152, especially pp.59-63. See also Hartshorne (1958).

136. Lenoir (1981), p.127.

137. For example, Crosland (1967) pp.104-113, seems to do no injustice to his subject in making Humboldt out to be a representative member of the Society of Arcueil.

138. Humboldt (1821-25) 1, p.V. In the translator's preface, p.III,this inelegant sentence is paraphrased as:- "... raising the mind to general ideas, without neglecting individual facts."

139. Cannon (1978), p.75.

140. "Goethe noted with satisfaction on receiving the first complimentary copy of the "Essai politique sur l'île de Cuba" that the author (Humboldt) had not omitted "pointers to the incommensurable" in spite of the tremendous amounts of statistics." Meyer-Abich (1967), p.106.

141. Cannon (1978), p.77.

142. See, for example, Forster (1778), p.60.

143. Humboldt (1814-29) 2, pp.32-39.

144. For Tobias Mayer's contribution to navigation and astronomy, see Forbes (1980), Chap. 2.

145. Humboldt (1820), p.3.

146. Crosland (1967), pp.264-5.

147. Cannon (1978), p.96, points out that it was unlikely that a Humboldtian science of measuring physical variables could have come into existence before the last two decades of the eighteenth century due to the available instruments being too crude.

148. Robinson and Wallis (1967).

149. George Harvey in the Encyclopaedia Metropolitana article on "Meteorology" (1832) - quoted by Cannon (1978), p.95.

150. Humboldt (1807a), p.32.

151. *Ibid*. p.42.

152. See the "Tableau Physique" and Humboldt (1821-5) 1, p.158.

153. *Ibid*.

154. Humboldt (1850), p.278. See also Stearn (1959).

155. Humboldt (1807), p.31.

156. _Ibid_.

157. Humboldt (1850), p.217.

158. _Ibid_. pp.220-221.

159. Humboldt (1821-25) _1_, p.158.

160. Humboldt (1850), p.217.

161. Lenoir (1981), p.127.

162. _Ibid_. pp.172-3.

163. For a description of this tradition see Whittaker (1962), pp.4-9.

164. Grisebach (1872a) _1_, pp.9-14.

165. _Ibid_.

166. Humboldt (1807a), p.15.

167. Willdenow (1805), p.399.

168. Humboldt (1807a), p.17.

169. _Ibid_. pp.18-19.

170. For a detailed account of the development of physiognomic and floristic technique in the classification of vegetation, see Whittaker (1962). For an account of the utilisation of floristic analysis by one of the most important European schools of vegetation science, see Becking (1957).

171. For Hooker's attitudes to Humboldt, see Stearn (1959). For Humboldt's influence on Darwin, see Theodorides (1968) and Egerton (1970). For Humboldt's influence on the exploration of the American West, see Goetzman (1965).

172. My account of the development of Humboldtian plant geography has the same form as the more detailed account of the origin of molecular biology supplied by Mullins (1972).

173. Humboldt (1807a), p.15; (1821-25) _1_, p.XXIV.f.

174. He did however exercise his right as a member of the Berlin Academy to lecture (on physical geography) at the University of Berlin, Kellner (1963), p.115.

175. See Braun (1954b). Braun concludes:- "Von Humboldt was perhaps the principal patron of intellectual endeavours of his age."

176. There are several published volumes of Humboldt's correspondence, see Beck (1959), pp.429-35. His letters to Varnhagen alone fill a substantial book, Humboldt (1860).

177. Sanders (1975), p.215. See also Schouw (1823), p.III. There is a longer biography of Schouw in Danish, Christensen (1923), which I have not consulted.

178. Schouw (1818). The title is roughly translatable as "Some remarks on Humboldt's work in plant geography".

179. Sanders (1975), p.215.

180. Schouw (1839).

181. Ibid. 1, p.VIII.

182. Ibid. 1, p.IX. I have been unable to locate either the second or the third volume.

183. Ibid. 1, p.1 (1st supplement).

184. Schouw (1823), p.165 - the nomenclature was apparently first proposed in an earlier (1822) Danish edition of this work, see Whittaker (1962), p.9.

185. It is probably fairer to say that Schouw made no consistent distinction between flora and vegetation. He studied both together, see Schouw (1826). In this he differs from Meyen, Kerner and the others I have identified as Humboldtian plant geographers. But, as Schouw himself put it:- "A Science is not established at once; its first ideas exist, are rejected, are touched upon cursorily, or are treated of without its being foreseen that these ideas will, in their time, form a self-existent branch of our knowledge." Schouw (1826), p.161.

186. See Browne (forthcoming) pp.81-82.

187. Grisebach (1838), p.160. The translation is from Clements (1916), pp.116-117.

188. See, for instance, Clements (1916), pp.125-130.

189. Kuhn (1962), pp.53-57, see also Brannigan (1981).

190. For an account of Humboldt's patronage of Meyen, see Jahn (1968), p.84.

191. Meyen (1846).

192. Ibid. p.27.

193. Jahn (1968), p.84.

194. Meyen (1846), p.3.

195. *Ibid*. p.8.

196. For the use of botanical arithmetic in floristic plant geography beyond Humboldt, see Browne (forthcoming) pp.77-89.

197. Meyen (1846), p.8.

198. *Ibid*. p.98.

199. *Ibid*. p.1.

200. The best biographical source for Grisebach is Stearn (1965). All biographical information is from this source unless otherwise stated. Also useful for Grisebach is Balfour (1882).

201. Balfour (1882), p.14.

202. For Kunth and his association with Humboldt, see Stearn (1968).

203. Grisebach (1843-46).

204. Balfour (1882), p.16.

205. Grisebach (1872a).

206. Grisebach (1872b).

207. Grisebach (1838), p.60. See Clements (1916), pp.116-117.

208. Grisebach (1849), p.418.

209. Grisebach (1846a), p.96.

210. Grisebach (1846b), pp.132-3.

211. *Ibid*. p.135.

212. The relative weighting to be given to physiognomic and floristic criteria was, as we shall see, in later chapters, a major source of controversy in vegetation science.

213. Kerner (1863), I have used Conard's (1951) translation of *Das Pflanzenleben der Donauländer*, Conard (1951) p.5. For biographical details of Kerner, see Kronfeld (1908).

214. Conard (1951) p.V.

215. *Ibid*. p.9.f.

216. *Ibid*. pp.4-5.

217. *Ibid*. p.3.

218. Ibid. p.10.

219. Ibid. pp.196-205.

220. Heer (1835); Thurmann (1849); Sendtner (1854); Lorenz (1858); and Hult (1881). Thurmann provides a clear definition of the difference between flora and vegetation:-

"A region's flora comprises an enumeration and description of all its species without reference to their abundance considered from a purely phytographic point of view;... a region's vegetation is its plant life which consists of species of the flora found in varying quantity and size some prominent, others scattered and merging into the background;.... To reach a thorough understanding of vegetation the flora must first be understood, but the flora may be studied without an exact and complete knowledge of vegetation. Thus a region's flora and its vegetation are two quite different things which should not be confused."

Trans.Duff (1980) p.44. However, as we have seen, Duff is wrong in his statement, p.26, that Thurmann was the first formally to distinguish floristic botany from the study of plant associations.

221. For biographical detail of Lecoq, see Chassagne (1928).

222. Lecoq (1854), 1, p.V.

223. Ibid. p.7.

224. Ibid. p.VII.

225. Ibid. pp.14-112.

226. Ibid. 4, pp.58-84 (sociabilité), pp.85-90 (association).

227. De Candolle (1855), 1, p.I.

228. Ibid. 1, p.419.f. See also 2, pp.1175-6.

229. Ibid. 1, p.419. Tobey's statement, Tobey (1977) pp.100-1, that De Candolle denied the possibility of the study of vegetation is erroneous. De Candolle was following another tradition of botanical practice but he acknowledged the existence of a vegetation science.

230. I am not, of course, arguing that Humboldt was not also important to the development of floristic plant geography. See Browne (forthcoming), Chap. 3, for an assessment of his influence. Nor am I suggesting that De Candolle's use of Humboldt is in any way illegitimate or a misreading. However the novel concern with vegetation is a characteristic aspect of Humboldt's work and there existed two traditions of plant geography in the nineteenth century - one of which springs from Humboldt's studies of vegetation. The other extends through Humboldt into the Linnean era.

231. For exemplifications of the British type of interest in floristic plant geography, see Watson (1835, 1847-59) and the introduction to Hooker (1853-5).

232. This presumably explains the almost complete neglect of vegetational plant geography by English-speaking historians of science. There is, however, it should be noted, a short description of the vegetation of the British Isles in Watson (1835), pp. 34-60. Also Darwin's most Humboldtian work (1839) contains several descriptions of the vegetation of South America. It is very likely that other examples could be found. But after 1850, the British emphasis seems to have been almost entirely on species distribution.

233. Hinds (1843); Heer (1935). For biographical details of Heer, see Anon. (1886).

234. Hinds (1843), pp.116-119.

235. Heer (1835), p.1 - the last sentence is from a footnote on the same page.

236. Von Post (1842), p.97; (1844), p.113; (1851), p.110. See also Hult (1881).

237. Whittaker (1962), p.24. A list of biographical sources for Hult is to be found in Barnhart (1965) 2, p.217.

238. See Godwin (1977), p.8, also Oswald (1959).

239. By "self-conscious ecology" I mean the activity practised by workers who called themselves "ecologists" and their activity "ecology". The term is borrowed from Allee *et al*. (1949), pp.42-43.

240. Hult (1881).

241. *Ibid*. p.1. I am greatly indebted to Ms. Sigridur Oladottir for providing me with a translation of this and the other passages quoted from Hult.

242. *Ibid*. p.2.

243. For the characteristics of the Uppsala school, see Whittaker (1962), pp.23-38. The Scandinavians rejected the inclusion of habitat factors within the definition of the association (Flahault and Schröter, 1910) using arguments very similar to those of Hult (Du Rietz, Fries and Tengwall, 1918).

244. Hult (1881), p.9.

245. Warming (1895a), Schimper (1898), Drude (1896); for comments on the institutionalisation of ecology, see Duff (1980), Chap. 2, Lowe (1976) and Cittadino (1980).

246. Godwin (1977), p.8.

247. Rubel, one of Schröter's students, has traced a tradition of research into the morphology of plant communities. His list of personnel contains several names I have mentioned above, viz. Humboldt, Grisebach "die Väter der Pflanzengesellschaften", Schouw, Lorenz, Lecoq, Kerner, Hult, Schröter, Sernander, and Warming, Rubel (1921), p.19.

248. Tansley (1939), p.532.

249. Cited in Godwin (1977), p.8.

250. I have quoted from the English translation of Schimper's book, Schimper (1903), p.162.

251. Ibid. p.161.

252. As we have seen, the maps given in books on plant geography frequently well exemplify the conventions of the cognitive framework which has produced them.

253. The best description of these changes is to be found in Cittadino (1981), but see also Green (1909).

254. Cittadino (1981), p.88.

255. Ibid. p.89.

256. Balfour (1882), p.18.

257. Cittadino (1981), p.2.

258. Schimper (1903), p.VI.

259. Cittadino (1981), p.151.

260. Schimper (1903), p.VI.

261. For an account (somewhat partisan) of Warming's career in ecology, see Goodland (1975). See also Müller (1976) and Tansley (1927).

262. Warming (1909), pp.2-3.

263. Tobey (1981), p.104, claims that the English translation "introduced a Humboldtian nuance into (Warming's) Darwinian theory". Thus Tobey argues that it cannot be said that Warming supported the idea of definite communities in the Humboldtian sense. But Müller (1976), p.182 translated the following passage directly from the Plantesamfund:-

"To answer the question: why each species has its own habit and habitat, why the species congregate to form definite communities, and why these have a characteristic physiognomy". One can see that the passage I have quoted from the English translation, note 262, is very faithful to the author's original intention.

264. Warming (1909), pp.2-6.

265. Tobey (1981), pp.102-4. Tobey provides little evidence for his separation of plant geography into a "mechanist" and "idealist" tradition. Tobey errs also in identifying Warming completely with the New Botany. Warming's first research was in taxonomy and floristics and he continued this line of work throughout his life. He published a very successful text-book on systematic and floristic botany (1895b).

266. Müller (1976), p.182.

267. Tobey (1981), p.103. Note that, contra Tobey, the ontological existence of plant communities is not necessarily dependent on cooperation between the constituent plants. Social integration may just as easily be held to arise as a by-product of competition - see, for instance, Clements (1935), pp.32-5.

268. Warming (1909), p.369 and p.370.

269. Zaunick (1959), p.138.

270. See Drude (1890a), p.IX. The Handbuch der Pflanzengeographie was dedicated to Grisebach.

271. Drude (1890a), p.28.

272. Drude (1890b), p.35.

273. Pound and Clements (1898a), p.4. The relationship between Drude and the Nebraskans is described by Tobey (1981), pp.57-70 and pp.87-99.

274. For the history of the Nebraskan "school", see Tobey (1981).

275. This point is elaborated upon by Cannon (1978), pp.76-82.

276. Ben-David (1971), Chapter 7.

277. Cannon (1978), pp.73-110.

278. See, for example Stearn (1960).

279. Cannon (1975) noted this fact, p.106.

280. For example, Egerton (1976), p.340.

281. Tansley (1927), p.55; Cowles (1901), pp.73-77.

282. Worster (1977), p.198.

283. Goodland (1955), p.241.

284. Godwin (1977), p.8.

CHAPTER 2

1. Kerner von Marilaun (1863), translated in Conard (1951), pp.4-5 - see discussion of Kerner's relation to Humboldtian botany in the previous chapter.

2. Nichols (1923), p.17, for example, proposed the following definition:-

   "...the association may be described as a vegetation-unit characterised by its essentially constant physiognomy and by its essentially constant floristic composition, at least with regard to dominant species".

   A similar definition was given by Du Rietz (1929), p.624.

3. Tansley (1920), pp.120-1.

4. Weaver and Clements (1938), p.89.

5. Conard (1939), p.10.

6. Van der Maarel (1975), p.213.

7. Flahault and Schröter (1910), trans. in Pavillard (1935), p.211.

8. Whittaker (1956), p.30.

9. Clements (1905), p.229.

10. For a comment on what some of these terms mean in their different contexts, see Egler (1942). I will use the term "phytosociologist" to refer specifically to members of the Uppsala or Zurich-Montpelier schools.

11. For remarks on the centrality of classification to the constitution of knowledge, see Bloor (1982). For an elegant empirical study of two different scientific classificatory practices, see Dean (1979).

12. See, for example, Tüxen (1950).

13. Compare Conard (1935), with Weaver and Clements (1938), pp.508-16. This comparison is borrowed from McIntosh (1958), p.116.

14. See, for example, Just (1939), and Shimwell (1971), especially introduction. I shall use the term "school" quite informally throughout the chapter - meaning a more or less loosely socially and/or geographically defined group of investigators sharing the broad principles of a common research programme. As an illustration of the informality with which I will use this term, I will refer to Zurich-Montpelier phytosociology as a "school" and I will use the same term to refer to the Sigmatists, who are, strictly speaking, a sub-group of the former.

15. Whittaker (1962).

16. Ibid. p.3.

17. See the detailed discussion of various schools in Whittaker (1975).

18. Whittaker (1962), pp.72-78. See also Sears (1956).

19. Whittaker (1956), p.72; Sears (1956).

20. I use the term "conventional" in the sense in which it is employed by Barnes (1981). I will argue that the different classification systems are socially sustained and not uniquely determined by input from the natural world.

21. For instance, its applications to tropical vegetation have tended to be more physiognomic than the European applications, see Emberger et al. (1950) and Mangenot et al. (1948).

22. Allee et al. (1949), pp.42-43. See previous chapter, footnote 239, for an explanation of this phrase.

23. My biographical information on Braun-Blanquet has been taken from Weadcock and Dansereau (1960), Lebrun (1975) and de Bolòs (1982). Braun-Blanquet died in 1982.

24. For the early history of the Zurich-Montpelier school, see Whittaker (1962), pp.9-23 and Westhoff and Van der Maarel (1973), pp.620-5.

25. As in Schröter and Kirchner (1902).

26. See, for example, Braun-Blanquet (1913), Braun-Blanquet and Farrer (1913).

27. Flahault (1901). Determination by dominant species is at least partly physiognomic, since the dominants are usually of a different growth-form from the subordinates.

28. Van der Maarel (1975), pp.213-4.

29. Brockmann-Jerosch (1907), Gradmann (1909).

30. Pavillard (1920), Braun-Blanquet (1921); Braun-Blanquet and Pavillard (1922).

31. Braun-Blanquet (1928).

32. Whittaker (1962), p.15.

33. The story of Braun-Blanquet's personal involvement with the Station is told in Braun-Blanquet (1968).

34. For an appreciation of the significance of the Sigmatist approach see Van der Maarel (1975).

35. Simberloff (1980), p.15, see also Moore (1983).

36. For biographical details of F.E. Clements, see E. Clements (1948), Ewan (1971), Sears (1973) and Tansley (1947).

37. For biographical details of Bessey, see Ewan (1970).

38. For Bessey's relation to the New Botany, see Overfield (1975).

39. For the impact of the New Botany in America, see Rodgers (1944), especially pp.1-7, 198-202, 226-50 and 304-20, and Farlow (1913).

40. For Bessey's teaching and the Botanical Seminar, see Tobey (1981), pp.9-23.

41. Pound and Clements (1900).

42. Ibid. p.4, Drude (1896). Roscoe Pound was shortly to abandon botany for a distinguished career in law. He eventually became Dean of the Harvard Law School. For biographical details and an account of his early interest in botany, see Wigdor (1974).

43. Clements (1904, 1905).

44. The use of the metre quadrat had been pioneered seven years earlier by Pound and Clements (1898); for the background to their invention, see Tobey (1981), pp.48-53 and 57-60.

45. Clements (1916).

46. Tobey (1977), p.15.

47. Clements (1916), pp.124-128.

48. Ibid. p.180, Weaver and Clements (1938), pp.481-2. The reduction was achieved by regarding vegetation types formerly held as formations as "sub-climaxes" or "disclimaxes", i.e. stages toward climatic climaxes. Thus short-grass prairie became a disclimax association of true prairie.

49. Weaver and Clements (1938), p.481.

50. Becking (1957), p.428 regards the term "concrete" to be a technically inappropriate one for units such as those described by Clements. However I follow here the usage employed by both Clements and Braun-Blanquet who contrasted their respective positions in these terms.

51. Becking (1957), p.427.

52. This was the key point of the "developmental" or "concrete" view, see Clements (1916), p.125.

53. Braun-Blanquet (1932), p.366.

54. Clements (1916), p.125. For Braun-Blanquet's opposition to Clement's organicism, see Braun-Blanquet (1932), pp.315-6.

55. See Clements (1936), p.254. In this article Clements provided a synthesis of the views he had held for thirty years.

56. Ibid. p.255.

57. See Egler (1951), p.682.

58. Clements (1936), p.255.

59. Weaver and Clements (1938), p.497.

60. I am here dodging the question of whether the Plains had been altered by the Indians.

61. Weaver and Clements (1938), p.488, Gleason (1901), pp.1-13.

62. Braun-Blanquet (1932).

63. For a vivid outline of the differences between British ecology and European phytosociology, see Poore (1955c), p.226.

64. Whittaker (1962), p.4 wrote:- "...one may well consider that British and American ecology form together a single tradition of no greater inherent diversity than the others."

65. See Carpenter (1939) and Whittaker (1962), pp.38-42.

66. Whittaker (1962), p.73. I must admit that the "ecology of ecologists" explanation is employed here as something of a straw man. I intend no strong criticism of either Sears or Whittaker. However, discussion of it helps my exposition since it illustrates the inadequacy of explanations of the character of ecological classification that are based entirely on considerations of the input the classifiers receive from the natural world. The patent incompleteness of the "ecology of ecologists" explanation highlights the importance of considering the cultural context of classification.

    On the other hand, I do not wish to argue that there is no substance whatsoever in the "ecology of ecologists" explanation. Experience of nature may not uniquely determine ecological classification but classifications are developed in the light of such experience. The importance of such input is indicated by the fact that actors frequently report difficulties when trying to apply a system devised for one sort of vegetation to another. We shall see, for instance, in the following chapters that ecologists experienced problems when trying to apply systems devised for Temperate America to either the Tropics or the Arctic. However it follows from the social nature of theory construction that such problems are always, in principle, soluble. See, for example, the solution devised by R.F. Griggs when faced by Arctic vegetation. This is described in Chapter four.

67. Braun-Blanquet (1932), p.VII.

68. Ibid. p.21. Braun-Blanquet did argue, however, that it was not always the "Linnean species as such that was most sensitive as a phytosociological indication but often its sub-species or eco-types".

69. Braun-Blanquet (1932), p.354.

70. Ibid.p.21 - the study of life-forms did allow a preliminary "rough characterization" of plant communities, but:- "They cannot however be used as permanent bases in the nomenclature and taxonomy of plant communities", ibid., pp.299-302.

71. Ibid. p.22.

72. This description of Sigmatist methodology is based on the detailed and critical accounts of Becking (1957), pp.426-447, Poore (1955a,b), and Westhoff and Van der Maarel (1973). Their accounts are fuller than any supplied by Braun-Blanquet himself. It should also be noted that the Sigmatists did much else besides classification. However floristic classification was a central part of their practice.

73. See Becking (1957), p.430.

74. Poore (1955a), p.288.

75. Ibid.

76. Braun-Blanquet (1949), p.7.

77. Braun-Blanquet (1932), pp.67-8.

78. Braun-Blanquet (1933).

79. Whittaker (1962), p.22.

80. The standard history of the New Botany is still Green (1909), but see also Cittadino (1981), especially Chap. 1.

81. For the reform of scientific education in the German universities and its effects, see Ben-David (1971), pp.108-133.

82. For the general adoption of German models of higher education in the United States, see *ibid.*, pp.139-162.

83. Quoted in Allen (1976), p.185.

84. Quoted in Huxley (1918), *1*, pp.403-4.

85. *Ibid.* *2*, pp.279-80.

86. The best biographical source for Bower is his own professional reminiscences, Bower (1938).

87. *Ibid.* p.21.

88. *Ibid.* p.102.

89. For a general account of Bonnier's work, see Davy de Virville (1970).

90. Bonnier and Douin (1911-1935), Bonnier and Layens (1886). For a note on Bonnier's floristic botany, see Stearn (1950).

91. See Davy de Virville (1970), pp.6-7.

92. See Hall and Clements (1923), pp.3-6.

93. Drude (1906), p.179.

94. Cittadino (1980), p.174.

95. Drude (1906), p.183.

96. This tendency of the nineteenth-century German University system to produce more young academics (Privatdozenten) than there were academic careers for is well documented, see Busch (1963). Zloczower (1966) discusses the effects the resulting competition had on research activity in physiology.

97. Cittadino (1981), p.1.

98. Huxley (1918), *1*, p.403.

99. For the importance of Engler and his school at the end of the 19th century, see Green (1909), pp.126-7, also Stapf (1931); for the importance of Edinburgh in British teaching of taxonomy at this time, see Bower (1938), p.58.

100. See Brockway (1979) and Bower (1938), p.26. Bower explained the British neglect of the New Botany as being the result of a preoccupation with Imperial duties on the part of the leading British botanists.

101. Such a shift of research interest might be tactical if the competitive situation in the adopted field was easier than in the original one. Physiology, both plant and animal, was especially overcrowded in the decades after 1880. Ben-David and Collins (1966) have analysed these factors in the development of psychology which was produced by an immigration of personnel from physiology to philosophy. Duff (1980), pp.30-37, makes several tentative remarks as to migration and cross-fertilisation between physiology and plant geography as a possible origin for a distinctive discipline of ecology. He gives little evidence for his assertion, but it seems likely that he is substantially correct. See also note 125 below.

102. Sanders (1975), p.166.

103. An Extraordinary Professor in a German university was one who had a sub-department within an institute or department headed by a full professor. In other words, Schimper still had a rung of the career ladder to ascend. Thus a shift in research interest at this time might well have been tactical in Ben-David and Collins's sense - see note 101 above. To establish this would require, however, a special study of Schimper and other similar cases.

104. Schimper (1898).

105. Cittadino (1981), p.112.

106. Retention of methodologies gained in physiology would also be tactical if the scientific status of phytogeography was lower than that of physiology, see Ben-David and Collins (1966), pp.459-61. Like Schimper, Haberladt still had rungs of the career ladder to climb. Although he was a full professor, his chair was at the University of Innsbruck - not one of the principal German universities and often a stepping-off point for a move to a more prestigious institution.

107. Ecology never, in fact, quite succeeded in fully identifying itself with the New Botany. It has always been regarded as being on the traditional side of the botanical profession. The persistence of such categorisations was brought home to me when I held a fellowship at the University of Canterbury, New Zealand. The Botany Department there fielded two soccer teams - the Trads and the Mods. As an honorary ecologist, I was invited to play for the Trads.

108. For a description of Schröter's teaching, see Tansley (1939), pp.531-4; for Flahault's interest in floristic botany, see Shene (1935), p.176. For the importance of Schröter and Flahault as "fathers of the Zurich-Montpelier school" of phytosociology, see the previous chapter.

109. Stafleu (1971), p.267, Braun-Blanquet (1949), p.7.

110. de Bolòs (1982), p.196.

111. Braun-Blanquet (1932), p.21.

112. Moss (1910). For biographical details of Moss, see Tansley (1931) and Crump (1931).

113. Gradmann (1909). Although this chapter has concentrated on the floristic systems as set out by Braun-Blanquet, it should have been noted that he was by no means the only advocate of such a system in the first decade of the twentieth century. As is consistent with floristic analysis being a piece of professional group strategy, it was a collective movement, involving Gradmann, Pavillard and Brockmann-Jerosch, among others associated with Schröter or Flahault.

114. Moss (1910), p.35.

115. See Becking (1957), p.467. Note that the meaning of "synécologie" is different from the Anglo-American "synecology". To an English speaker, synecology is the study of communities in all its aspects- to a Frenchman, synécologie is the study of community habitats.

116. See, for example, Braun-Blanquet (1924). However this paper also well evidences how the study of habitat factors was secondary in Braun-Blanquet's eyes to the floristic identification of associations.

117. Braun-Blanquet (1932), p.82. The German phytosociologist, R. Tüxen, a pupil and close associate of Braun-Blanquet (see Braun-Blanquet (1969) and Barkman (1981)) explicitly argued that the plant was a better measure of habitat factors than any instrument, Tüxen (1942).

118. Braun-Blanquet (1932), p.82; emphasis added.

119. Braun-Blanquet expressed his disagreement with this investigative strategy:- "Those investigators who regard synecology as the foundation of phytosociologic classification and indeed of the whole structure of plant sociology, must not forget how insecure that foundation still is", <u>ibid</u>. p.81.

120. Moss (1910), p.26.

121. Overfield (1975), pp.164-168.

122. Pound and Clements (1900), p.4. I have consulted the second edition. The first edition appeared in 1898 but is very rare. Pound (1896) reviewed Drude's book enthusiastically when it appeared.

123. Clements (1905), pp.1-2. Cowles made a similar identification of the two subjects:- "It is coming to be realised that the problems of physiology and ecology are essentially identical ... in all respects ... The method of approach has differed with the point of view, and it is the physiologist who has given most emphasis to the fundamental importance of experimentation. The ecologist, on the other hand, has brought in the rich contribution of field observation. It is only recently that each has recognised the imperative necessity of the method of the other, and it now seems possible to predict that the fundamental method of the future is to be field experimentation combined with observation." Cowles (1908), p.265.

124. Clements (1905), p.103.

125. Clements's work in physiology was never accepted as competent by established plant physiologists, see Blackman and Tansley (1905), pp.233-7. The claims made by Clements as to the close kinship between his work and that of physiologists are most plausibly interpreted as part of a tactical programme designed to enhance ecology's scientific prestige by "borrowing the methods of a high-status field", Ben-David and Collins (1966), p.460. See also note 101 above. Ben-David and Collins's work has stimulated a considerable amount of further study, and a considerable bibliography on intellectual migration and the transfer of methodologies is now available. Mulkay (1972), Chaps. 4 and 5, Mullins (1972), Mulkay (1974), Whitley (1974) and Robbins and Johnston (1976) provide examples of a variety of approaches. The tactical advantage of being seen to apply the methods of a higher status discipline within a lower status one are clear from all the above studies. See also Schon (1963) for a less overtly sociological formulation of the same phenomenon.

126. Clements (1905), p.2.

127. Clements (1908), p.253.

128. The epithet "medieval" was used by Bessey to describe orthodox taxonomy at the same conference that Clements delivered the paper from which the previous quotation is derived, Bessey (1908), p.252.

129. Clements (1920), p.56.

130. Clements (1908), p.259.

131. The advantage of splitting was that it allowed taxonomists to create new species. A taxonomist's reputation depended on the number of new species he created. For a sympathetic study of an inveterate "splitter", see Rodgers (1944a).

132. Clements (1920), p.56. The splitting of genera was particularly troublesome to non-taxonomists since it forced them to discard long familiar plant names and learn new ones.

133. Cowles (1908), Bessey (1908).

134. Clements (1920), p.56.

135. For the general background to the Land-Grant Colleges and their social situation, see Eddy (1956) and Ross (1942). For studies of the constraints, upon scientific activity in these or related institutions, see Rosenberg (1972, 1979) and Rossiter (1979). It must also be remembered that American opinion, in the East as well as the West, was in the whole suspicious of pure research, especially if public funds were involved, Daniels (1967). The Land-Grant Colleges, thus, intensified a quite general social pressure encouraging directly applicable scientific research.

136. Overfield (1975), pp.170-76, see also Tobey (1976).

137. See for example, Bessey (1886, 1888, 1894, 1895). Tobey (1976), pp.719-720 and Overfield (1975), p.173 give fuller lists of publications by Bessey relevant to these subjects.

138. Tobey (1976), pp.720-22.

139. E. Clements (1948), p.266.

140. Clements (1905), p.14.

141. Eddy (1956), p.84.

142. E. Clements (1948), p.266.

143. Clements, "Annual Report of the Minnesota State Botanist" (1910) (not seen) - quoted in Clements (1920), p.9.

144. See Rosenberg (1979), p.156. The pressures and aspirations which produced McCollum's and Pearl's rejection of the role forced upon them by the milieu of the experimental station are well described in Rosenberg (1972).

145. Clements (1920).

146. Ibid. p.330.

147. Ibid. pp.227-40.

148. Ibid. pp.331-4.

149. E. Clements (1948), p.226.

150. E. Clements (1960), p.230.

151. Clements (1935a).

152. Ibid. p.355.

153. For the general increase in interest in conservation occasioned by the Drought and the New Deal, see Swain (1963). For the involvement of the Nebraskans in drought-inspired conservation schemes on the Plains, see Tobey (1981) Chap. 7.

154. See note 135 above.

155. See Tobey (1976) for the practical orientation of Bessey's research and pedagogy.

156. The conflict between disciplinary allegiance outside the local context and the practical orientation essential within it is described by Rosenberg (1972), pp.185-90 and 199-203. As Rosenberg expressed it elsewhere (1979), p.144:- "In the hierarchy of scientific achievement, applied science possessed a ... problematic quality: enshrined in the formulas of conventional rhetoric, the applied scientist was nevertheless part of a scientific world in which abstractness generally correlated with status. The utility so appealing to mid-nineteenth century Americans constituted a dubious virtue in the world of pure science."

157. Letter, Clements to Tansley, July 30th 1905. Box 1, Tansley Papers.

158. See, for example, Clements and Shelford (1939), pp.1-5.

159. See Clements (1902a,b). The uncompromising character of many of Clement's prescriptions for ecology may be readily appreciated from these articles.

160. Clements (1905), p.6.

161. Ibid. p.20.

162. McMillan (1892).

163. McMillan (1899).

164. Letter, McMillan to Clements, Jan. 3 1907, Bessey Papers, University of Nebraska Archives, quoted and discussed in Cittadino (1980), pp.24-25.

165. McMillan (1897).

166. Drude (1905), p.188.

167. See Cittadino (1980), pp.21-25 and Gleason (1961), pp.121-22.

168. Quoted in Rosenberg (1979), p.151.

169. Even F.E. Egler, an arch-opponent of Clementsianism was forced to acknowledge that Clements was "a practical realist ... who impressed the soil conservationists, agronomists, and range managers with his down-to-earth understanding of land management.". Egler (1951), p.677.

170. A "Grayian" species is one of the sort used by Asa Gray, the dominant figure of nineteenth-century American taxonomy. A Grayian species was a broad category encompassing a fair degree of morphological variation.

171. See Cowles (1908), Clements (1908) and Bessey (1908).

172. Compare Webb (1959), p.29.

173. See, for instance, Clements (1902a).

174. Letter, E.I. Rose to J.T. Curtis, Sept. 6 1948, Curtis Papers.

175. See Weadock and Dansereau (1960), p.11.

176. Paul (1972), pp.1-28.

177. Quoted in Ibid. pp.27-28.

178. Ibid. p.25.

179. Ibid. p.20. This point is relevant in the present context due to the links between Montpelier and Zurich. The Station at Montpelier was in Swiss ownership; Braun-Blanquet's programme had been first devised in Zurich, Braun-Blanquet (1932), p.vii.

180. See Paul (1980) and Shinn (1980).

181. Paul (1980), pp.158-66.

182. Nye (1975), p.291.

183. Paul (1980), p.161,

184. Ibid. p.162.

185. Shinn (1980), pp.302-315.

186. This hierarchy was enshrined in the official aims of the Montpelier station, see Weadock and Dansereau (1960), p.3.

187. Ibid. p.13.

188. Westhoff and Van der Maarel (1973), p.622. Tüxen's interest in application is emphasised by the fact that he became editor of the journal Angewandte Pflanzensoziologie (Applied Phytosociology).

189. Braun-Blanquet (1932), p.26.

190. de Bolòs (1982), p.193.

191. For example, Braun-Blanquet (1949, 1952); the quotation is from the former, p.6.

192. Braun-Blanquet (1949), pp.7-8, 14-16.

193. Braun-Blanquet (1935); Weadock and Dansereau (1960), p.9.

194. Weadock and Dansereau, p.9.

195. See note 135 above.

196. Clements (1916), p.3.

197. _Ibid_. p.6.

198. Clements and Shelford (1938), pp.20-21.

199. For example, Clements, Weaver and Hanson (1929), p.314.

200. For the American vogue of Spencer, see Hofstadter (1955a), Chap. 2.

201. Pound (1954), p.113.

202. Clements, Weaver and Hanson (1929), p.314.

203. Clements (1935), p.35.

204. _Ibid_.

205. Smuts (1927), p.349.

206. Clements and Shelford (1939), p.23.

207. Quoted in _ibid_. p.24.

208. _Ibid_. p.21.

209. Clements to Tansley, Sept. 30 1916, Box 2, Tansley Papers.

210. The classic text on the history of the Great Plains is Webb (1959), 2nd ed. I have leant upon Webb's account extensively. More detailed and up to date is Kraenzel (1955).

211. The detailed history of this and other ranching problems on the plains is set out in U.S. Secretary of Agriculture (1936).

212. For the ideological background to the Homestead Act, see Hofstadter (1955b) Chap. I.

213. Kraenzel (1955), pp.137-48.

214. See Morgan (1971), Chap. I.

215. For the history of agrictultural discontent, see Saloutis (1951) and Burden (1965). The history of agriciltural discontent is also the history of populism, see Hofstadter (1955).

216. The tension between the welfare demands of populist and other references and the entrenched support for individualism and laissez-faire is described in Fine (1956).

217. For the legal problems surrounding water use, Webb (1959), pp.431-52.

218. For legislative attitudes to the rancher, see Webb (1959), p.411. For the sanctity accorded the small farmer against all other landusers, see Carstensen (1958).

219. Lamar (1974), p.510.

220. For the effect of New Deal legislation on landuse in Nebraska, see Berberet (1970).

221. Clements and Shelford (1939), p.3.

222. For a general study of the ideological connotations of ecologists' holistic rhetoric,see Lowe and Warboys (1980).

223. This attitude on land-use and conservation is well documented by Hayes (1959).

224. Akin (1977), esp. Chap. 4.

225. Quoted in ibid. p.10, Taylor by training an engineer was the founder of the scientific study of management, see Taylor (1911).

226. Akin (1977), Chap. 2.

227. Quoted in Duff (1980), p.119.

228. See Allee et al. (1949), Chaps 1&2.

229. Clements and Shelford (1939).

230. For Shelford, see Miller (1977) and Kendeigh (1968).

231. Clements and Shelford (1939), p.6.

232. Clements affirmed this similarity, ibid. pp.144-6.

233. Worster (1977), pp.326-7.

234. Russett (1966), p.164.

235. Emerson (1954), pp.74-75.

236. Since I began this study, two other historians have written on ideological aspects of American ecology - Ronald Tobey (1981) and Andrew Duff (1980). Duff's conclusions are broadly similar to my own. However his account is very general and his analysis refers to American ecology as a whole rather than to Clements directly, or indeed to any particular group. Duff distinguishes little heterogeneity either within ecology or within the cultural backgrounds from which it sprung and the social movements with which it was connected. My account, as offered here, is therefore more finely textured and more strongly contextualised than Duff's. However, within limits, our accounts reinforce and complement one another.

    There are more important points of difference between my treatment of Clements and that offered by Tobey. Tobey identifies a shift in the ecological theorising of Clements and his associates consequent upon the problems of the Great Drought. His analysis of Clementsian ideology amounts to an attempt to characterise this shift as ideological - as the altering of ecological knowledge to meet the new social goals offered to ecology by the New Deal, Tobey (1981), pp.202-13. I can see no evidence of such a shift. More importantly, I would argue that Clements's ecology was ideological throughout its entire career. I have attempted to adduce evidence that from its very inception Clementsian ecology was shaped by social interests. One might say that Tobey leaves still unfinished Mannheim's unfinished agenda.

237. Tobey (1981), pp.80-2 has argued that there is a necessary conflict between organismic and mechanist elements in Clements's work. But his a priori logical approach is borrowed from scholarship in the history of ideas and he pays no regard to the context of use, which is where I would argue the essential similarity lies.

238. Veblen (1921), pp.5-9, paraphrased and quoted in Akin (1977), p.21. Veblen was describing the national industrial system. Herbert Hoover, in 1921, described the same institution as "a single industrial organism", Akin (1977), p.13.

239. Clements (1920), p.16.

240. Clements (1935), p.41 et passim.

241. See, for instance, Allen (1976), p.241.

242. Letter, Clements to A.E. Tansley, Jan. 12 1906, Box 1, Tansley papers.

243. For an account of Henderson's political views, see Heyl (1968), also Paranscandola (1971).

244. For W.C. Allee, see Schmidt (1957).

245. See Peel (1971), pp.166-191 for a discussion of the conclusions Spencer drew from his organic conception of society.

246. A similar interventionist interpretation of Spencer was made by the American sociologist, Lester Ward, see Hofstadter (1955a) Chap. 4. For similarities between Ward and Clements, see Tobey (1981), pp. 84-86.

247. J.R. Commons, quoted in Hofstadter (1955a), p.34.

248. Ibid.

249. See note 215 above.

250. Hofstadter (1955b), p.64.

251. Clements shared much with other writers on society and nature in the West and Middle West. Coleman's (1966) essay on Frederick Jackson Turner, the most eminent historian of the American West, comments on the Spencerianism, organicism and environmentalism which characterised Turner's famous "Frontier Hypothesis". Turner was also interested, like Clements, in physiography and the natural divisions of the earth's surface. Turner had been, like H.C. Cowles, a student of the geologist T.C. Chamberlin. Coleman provides much evidence to support the view that Clements constructed his arguments using elements that were already in common political and scholarly use in the West and Middle West.

252. Clements and Chaney (1936), p.51.

253. For the difficulties encountered in the passage of land-use legislation, see Foss (1960) esp. Chap. 3.

254. Clements (1920), p.330.

255. Ibid. pp.330-4.

256. Taylor (1936), p.343.

257. Taylor (1935), p.304.

258. Ibid. p.303.

259. Ibid. p.296.

260. Taylor (1936), p.342.

261. Ibid. p.336.

262. Ibid. p.342.

263. For Malin's biographical details see Brodhead (1980) and Williams (1979). For his political and historigraphical views see Le Duc (1950), Bell (1972) and Johannsen (1972).

264. Malin (1955), p.346.

265. Malin (1953), p.219.

266 Malin (1946), p.93.

267. Malin (1952), p.37.

268. Malin (1955), pp.338-47.

269. Turner (1920).

270. Malin (1946), pp.32-46.

271. Malin (1950), p.296.

272. Malin (1952), p.30.

273. Malin (1952), p.33

274. Ibid. pp.32-33.

275. "The Plow that Broke the Plains" was a title of a film on the dust storms of the nineteen thirties. Malin regarded the film a deceitful libel on the homesteaders.

276. This is the title of one of Malin's books (1955).

277. Malin (1946), p.103.

278. Malin (1946), p.102.

279. For Malin's support of those who spoke of the New Deal in these terms, see Malin (1954), pp.237-62.

280. Malin (1946), p.99.

281. Malin (1946), p.104. The "brains trust" was a body of experts which advised Roosevelt during the New Deal.

282. Two important studies of the tension between individualism and collectivism in American social thought are Peterson (1960) and Arielli (1964). Dated and somewhat partisan but still of interest in this connection is Wiltse (1935).

283. I emphasise the word "principle" because in practice, central direction of land use, although theoretically legitimate, might well be determinedly opposed by individualistic land-users in the regions. See, for example, Ardagh (1982), pp.244-5.

284. For collectivism in France and its ideological justification, see Zeldin (1973), pp.521-44. I do not, of course, mean to imply that France is not, in its way, an intensely individualistic country. However, the points I wish to stress are that the centralisation of the state is acknowledged to be legitimate and that the apparatus of central government has a monopoly of formal authority. However, as illustrated by the example of forestry, considered above, the state's power to act is frequently severely limited by intense individualism at the regional level. One might say that France is vertically collective but horizontally individualistic, see Hoffman (1963) and Gilpin (1968), pp.78-85. The American form of individualism is quite different. There the strong popular belief in individualistic virtue had led to demands for a minimal central government and strong regional autonomy. This theme of contrast between American and French statecraft and culture is, of course, a very old one - see De Tocqueville (1835).

285. For the French conservation movement, see Ardagh (1982), pp.336-46; for the technocrats, see Zeldin (1977), pp.1040-82.

286. The classic treatment of incommensurability is Kuhn (1962) and his "Postscript" in the second edition (1970). Collins and Pinch (1982) is an important recent study of, as they call it, "contemporaneous conceptual discontinuity".

287. Braun-Blanquet (1932), p.326.

288. Weaver and Clements (1938), p.104.

289. Braun-Blanquet (1932), p.305.

290. We will see examples of the rejection of random sampling for this reason in chapter four.

CHAPTER 3

1. Tansley (1947), p.194.

2. Clements's isolation from his American colleagues was noted and commented on by one of his most enthusiastic supporters, the South African J.V. Phillips, see E.S. Clements (1960), pp.22-6.

3. For a description of the Clementsian coterie, see Tobey (1981), especially chap. 1. See also Sears (1969).

4. See McIntosh (1976), p.354. McIntosh is not correct, however, in stating that Clements coined the term "geotome" to refer to a common or garden shovel. The instrument referred to was a soil auger.

5. Tansley (1947), p.196.

6. See Burgess (1977), p.7 for a complete list of the office-bearers of the Ecological Society of America, prior to the Second World War.

7. E.S. Clements (1960), p.123, Tansley (1947), p.147.

8. One of Clements's very few comments on Gleason's criticisms of his view consisted of the following:-

   "In contrast to this (Clements's theory of the community bond) stands the "individualistic" concept of the community, which has been proposed by Gleason (1917, 1926). This appears to involve a confusion of ideas as well as a contradiction in terms; it has been adequately characterized by Tansley (1920: 126) and requires no further consideration here."

   Clements, Weaver and Hanson (1929), p.315.

9. See Sprugel (1980).

10. The orientation of the University of Chicago toward pure research, as against immediate practicality, is well described in Storr, R.J. (1966), p.68 _et passim_. See also, Murphy and Bruckner (1976). John Merle Coulter, the first chairman of Chicago's botany department, shared this belief that pure science ought to be the special province of a university - see Rodgers (1944), pp.138-40, 236-7, 294-7. Coulter was Cowles's PhD. supervisor, and his head of department.

11. Gleason (1926a), p.16.

12. Gleason (1931), p.78.

13. For an assessment of Gleason as a taxonomist, see Maguire (1975). Gleason was president of the American Taxonomic Society in 1938.

14. There have been several short impressions of Gleason published, notably Cronquist (1976), Maguire (1975) and Smith (1975). The best account of his theoretical work in ecology is McIntosh (1975). McIntosh's survey is detailed but says little about the historical development of Gleason's ideas or why he held the views he did. McIntosh was, as the following chapter describes, one of the ecologists who were responsible for reviving interest in Gleason's work in the fifties and sixties. His attitude is therefore, that Gleason advocated the individualistic hypothesis because it was true, as more recent research has revealed.

    For methodological reasons, I shall attempt to be neutral over the rectitude of the individualistic hypothesis, just as I was neutral over the existence of the plant community in earlier chapters.

15. For the institutionalisation of ecology in America, see Duff (1980) especially chap. 5.

16. This may be judged from the very full bibliography provided by Maguire (1975).

17. There is no complete published account of Gleason's life. I have been fortunate enough to be allowed access to a three-volume unpublished autobiography which Gleason wrote in his retirement, Gleason (1963-4). This is in the care of Henry Allen Gleason Jnr. My biographical information is drawn principally from this course. I have also drawn from an earlier much shorter unpublished autobiography held in the library of the New York Botanical Garden, Gleason (1944).

18. Gleason (1944), p.1.

19. _Ibid_. p.3. These early notebooks are no longer extant, as far as I am aware, but no doubt they already bore the impression of the patient, studious attention to detail and concern for accuracy which were to be characteristic of all of Gleason's later scientific work.

20. Gleason (1963-4) _1_, p.40.

21. _Ibid_. p.71.

22. Burgess (1971), p.7.

23. Gleason (1963-4) _1_, p.72. For Adams, see Raup (1959).

24. For S.A. Forbes, see Howard (1931).

25. McIntosh (1976), p.353.

26. McIntosh (1980). See also, Hutchinson (1963) and Smith (1926).

27. Forbes (1887), p.549. See also Forbes (1880).

28. Clements and Shelford (1939), p.14.

29. Forbes (1907), p.277.

30. See Vasey (1861).

31. Gleason (1963-4) 1, p.89.

32. Gleason (1964), p.8.f.

33. See Cittadino (1980), pp.173-4, Allen (1976), pp.240-3 and Lowe (1976) for accounts of these developments.

34. Gleason (1963-4) 1, p.78, see Gleason (1901).

35. *Ibid.* p.91. The papers by Cowles referred to are presumably Cowles (1901) and Cowles (1899) respectively.

36. MacMillan (1897).

37. Adams and Fuller (1940), pp.39-40.

38. Schimper (1898), Warming (1896).

39. Cowles (1901), p.77.

40. Warming (1896), pp.358-63 - the page numbers refer to the English translation (1909).

41. Cowles (1901), p.78.

42. *Ibid.* pp.78-9.

43. A peneplain is the level topography which is the theoretical end-point of erosion acting upon a raised land-mass. Mesophytic vegetation is vegetation adapted to conditions which are neither extremely dry (xeric) nor wet (hydric). In any given climate, extremes of dryness and wetness are often produced by an irregular uneroded young topography.

44. The best source for Davis's geomorphology is Davis (1909). Adams and Fuller (1940), p.39 wrote of Salisbury's "inspiring influence" on Cowles while Cowles was an undergraduate. Drury and Nisbet (1971) give an account of the structural similarities between Davis's theory of base-levelling and early American ecological theories.

45. Adams and Fuller (1940), p.39. Further biographical details for Cowles are to be found in Fuller (1939).

46. Tansley (1940), p.451.

47. Cowles (1901), p.73.

48. Ibid. p.79.

49. Transeau (1903), Whitford (1901), Cooper (1913, 1923, 1928) - these are only examples. See Sprugel (1980) for the names of more of Cowles's students.

50. Clements (1904), pp.105-113.

51. Gleason (1936a), p.42.

52. Such diagrams occur, for example, in Gleason (1910), p.104 and Gleason (1907), p.78.

53. Gleason (1963-4) 1, p.84.

54. Ibid. p.86.

55. Gleason (1944), p.11.

56. Fuller details of this episode in Gleason's career will be given later in this chapter.

57. Gleason (1963-4) 1, p.155.

58. Ibid. p.162.

59. For Burrill, see Rodgers (1968), Chap. 9.

60. Gleason (1904), p.19.

61. Adams (1902, 1905).

62. Gleason (1904), pp.97-98.

63. Kellerman, Gleason and Schnaffner (1914).

64. Gleason (1963-4) 1, p.149.

65. Ibid. p.73.

66. Ibid. p.155.

67. Ibid. p.162.

68. Gleason (1909c).

69. Gleason (1944), p.13. V.E. Shelford was also a very early pioneer of the application of Cowles's ideas to animal populations.

70. Clements (1905), pp.239-241. Clements coined the term "associes" to refer to successional stages leading up to the association.

71. Gleason (1909c), p.57. Clements employed the recapitulation analogy as late as 1916, Clements (1916), p.345.

72. Letter, Gleason to R.P. Wodehouse (Editor - Bull.Torr.Bot.Soc.) August 5th 1939. Gleason Papers.

73. Cowles (1911), pp.168-170.

74. Cowles, Whitford and Adams presented a paper entitled "The relation of base-leveling to specific differentiation" at the meeting of the naturalists of the central states at Chicago on December 27th, 1900. The proceedings of the meeting are listed in the Bot.Gaz. (1909) 31, p.72. I have not been able to trace a published version of this paper.

75. Gleason (1953), p.41.

76. Gleason (1963-4), 1, p.167.

77. Ibid. p.170.

78. Gleason (1944), p.15.

79. Gleason (1963-4) 1, p.180.

80. Ibid.

81. I have taken the following papers to be unequivocally ecological:- 1907, 1909a, 1909b, 1909c, 1910, 1912, 1913b, 1914, 1917a, 1917b, 1917c, 1918a, 1918d, and Gleason and Gates (1912). The following I have classified as floristic or taxonomic:- 1913a, 1913c, 1918b, 1918e. The last mentioned is a short abstract. Two papers I have classified in neither category:- 1908, 1918c. The "Botanical sketches" (1915a-c, 1916) - anecdotal account of his travels in the Asiatic tropics, I have likewise not included in either category.

82. Contra McIntosh (1975), p.253.

83. The three papers, together with an introduction, were given the overall title "On the biology of the sand areas of Illinois". Hart and Gleason (1907).

84. Gleason (1907), p.149.

85. Ibid. pp.159-60.

86. Ibid.

87. Gleason (1910), pp.67-69 et seq.

88. Pound and Clements (1898a).

89. Clements was later actively to oppose the introduction of statistical methods into ecology, see Tobey (1981), pp.180-4.

90. See, for example, Kofoid (1903).

91. Frey (1963), p.123.

92. See Lussenhop (1974).

93. There is a good account of Kofoid's work in Gleason (1963-4) 1, pp.115-7.

94. See, for example, Forbes (1907).

95. Gleason (1909a, 1909b, 1910, 1912, 1913b).

96. Gleason (1910).

97. *Ibid.* p.20.f., Gleason (1963-4) 1, p.188.

98. Cowles (1899, 1901), Cooper (1913).

99. Taylor (1912), p.113.

100. See Whittaker (1973).

101. Clements (1916), p.127.

102. Clements (1935), pp.254-5, 258.

103. Clements (1916), p.128.

104. For example, "Primula - Polemonium - Oxyria - phellium", Clements (1902a), p.17, was Clements's name for the "primrose rock cleft formation". (This would have been called an "association" in his later terminology.) The first three words are generic names - the last refers to the rock habitat.

105. Gleason (1910), p.42.

106. *Ibid.* p.37.

107. *Ibid.* p.37.f.

108. Clements (1905), pp.100-1.

109. Gleason (1910), p.35. Clements acknowledged the importance of vegetational "reaction" -that is changes produced in the environment by the vegetation but held that the overall climate was the primary determinant of the vegetation.

110. Gleason (1963-4) 1, p.191.

111. Clements (1916), p.3.

112. Ibid. p.145.

113. Gleason (1910), pp.112-6.

114. Gleason (1917c), p.479.

115. Gleason (1910), p.134.

116. Cooper (1926), p.393.

117. Ibid.

118. The term "consocies" was coined by Clements to refer to successional stages of a consociation. A consociation was an association dominated by a single species. See Clements (1936), pp.278-9.

119. Burgess (1977), p.7.

120. Gleason (1963-4) 1, p.190.

121. Ibid. p.183.

122. Burgess (1977), p.7.

123. Gleason and Gates (1912).

124. Livingston (1908).

125. See Livingston (1935) for a review of atmometer work in the United States.

126. Livingston and Shreve (1921) p.XI.

127. Coulter, Barnes and Cowles (1911) 2, p.2.

128. Livingston (1948), pp.233-4.

129. McIntosh (1983), p.108.

130. It is instructive to note that Livingston's work was accepted as competent by specialist plant physiologists - he became director of the Johns Hopkins Laboratory of Plant Physiology - whereas Clements's work was not - see Blackman and Tansley (1905), pp.233-7. F.F. Blackman was the "doyen of Cambridge plant physiology", Godwin (1977), p.12.

131. Livingston and Shreve (1921), p.5.

132. See Transeau (1908), Fuller (1911).

133. Gleason and Gates (1912), p.491.

134. Gleason (1963-4) 1, p.221.

135. _Ibid_. p.332.

136. _Ibid_. p.338.

137. _Ibid_. p.340.

138. The trip is described in Gleason (1963-4) _1_, pp.267-330.

139. Gleason (1915a, 1915b, 1915c, 1916).

140. Gleason (1915b), p.123.

141. Gleason (1917a, 1918d).

142. Gleason (1923a).

143. Gleason (1963-4) _1_, p.258.

144. _Ibid_. p.259.

145. Clements (1916).

146. Gleason (1910), p.463.

147. _Ibid_. pp.463-4.

148. Gleason (1910), p.36.

149. _Ibid_. p.35.

150. _Ibid_. p.41.

151. Gleason (1917c), p.474.

152. _Ibid_. p.464.

153. _Ibid_. p.471.

154. _Ibid_. p.466.

155. _Ibid_.

156. _Ibid_. p.480.

157. _Ibid_. p.473.

158. _Ibid_.

159. _Ibid_. p.468.

160. _Ibid_. p.469.

161. _Ibid_. p.473.

162. _Ibid_.

163. _Ibid_. p.465.

164. _Ibid_. pp.478-9.

165. _Ibid_. p.464.

166. _Ibid_.

167. The use of the word "hypothesis" to describe Gleason's individualistic concept seems to have been introduced by Cain (1939), p.190.

168. See, for instances, Webb (1954), Ponyatovskaya (1960), McIntosh (1967), Duff (1975), Worster (1977) and Tobey (1981).

169. Worster (1977a), p.6, Worster (1977), pp.217-42, Tobey (1981), pp.170-1.

170. The quotation is from Tansley's (1935) criticism of Phillips (1934, 1935):- "He (Phillips) is occupied for the most part in giving the pure milk of the Clementsian word, in expounding and elaborating the organismal theory of vegetation. This exposition ... is a useful piece of work, but it invites attack at almost every point."

171. I have been able to examine 26 of the 29 titles listed by Weaver in the bibliography of his major book, Weaver and Alberton (1956).

172. See Bergman and Stallard (1916).

173. Duff (1975), p.42.

174. McDougall (1931), pp.214-18.

175. Weaver and Clements (1929), p.2 _et seq_.

176. Clements (1907).

177. Nichols (1917).

178. There is a good biographical account of Nichols in Steere (1977), pp.330-2.

179. Nichols (1917), p.305.

180. _Ibid_.

181. _Ibid_. p.306, emphasis in original.

182. _Ibid_. p.349.

183. _Ibid_. p.306.

184. _Ibid_. pp.317-19.

185. *Ibid.* pp.312-13.

186. *Ibid.* pp.341-44.

187. Schimper (1898), p.173-6. See also, Cowles (1901), p.75.

188. Tansley (1916), p.203.

189. Cowles (1901), p.80.

190. Cowles (1911), p,161.

191. Cooper (1913), p.232.

192. *Ibid.* pp.1-2.

193. Cooper's reservations were that the trend toward the monoclimax was best thought of as "a variable approaching a variable" rather than an orderly, directed inevitable progression, Cooper (1926), p.405. The phrase quoted was originally Cowles's (1909), p.81.

194. Cooper (1926), p.394.

195. *Ibid.* p.399.

196. *Ibid.* p.410.

197. *Ibid.* p.394.

198. A strong similarity may be noted between the criticisms of Clements quoted here from Gleason (1917) and those to be found in Cooper (1926).

199. Gleason (1927), p.311.

200. Letter, W.S. Cooper to J.T. Curtis, March 25th 1946, Curtis Papers.

201. Gleason (1917c), p.464.

202. Cooper (1926), p.394.

203. Letter, W.S. Cooper to J.T. Curtis, March 25th 1946, Curtis Papers.

204. Nichols (1923), p.14.

205. *Ibid.* p.17.f.

206. Fuller (1918), p.386.

207. *Ibid.*

208. Nichols (1926), p.638.

209. Ibid. p.635.

210. Gleason (1939), p.93. That the tripartite scheme used here coincides with contemporary actors' categories is further evidenced by the following passage from Egler (1947), p.389:-

"The term association has become linked with a concept of a plant community that possesses a high degree of integration and organization. This concept was pushed to a ridiculous extremity when the community was identified with a biologic-organism. (the position of Clements) ... The bulk of the Americans have been middle-of-the-roaders who, nevertheless, still give the plant community such a high degree of integration that associations have a clear-cut distinction in time and space, and can be classified like biologic-organisms (the position I have described as the mainstream) ... Personally, the writer believes the association-concept ... to have caused serious confusion ... In its stead the writer adopts wholeheartedly ... The "individualistic concept" of the plant community as developed by Gleason ...

211. Gleason (1963-4) 2, p.2.

212. Ibid. p.22.

213. Gleason began the work on the New Britton and Brown (Gleason 1952a) in 1939.

214. Gleason (1963-4) 1, p.340.

215. Nichols (1923), p.12.

216. Gleason (1961), pp.82-3.

217. Gleason (1963-4) 1, p.342.

218. Gleason (1920).

219. Ibid. p.22.

220. Ibid.

221. Ibid. p.23.

222. Ibid.

223. It should be noted that the utility of random sampling was controversial among professional statisticians at this time. I am indebted to Mr. G. Cohen for this observation.

224. See, for example, Weaver and Clements (1938), p.11.

225. Gleason (1920), p.22.

226. Jaccard (1901).

227. Gleason (1920), p.28.

228. Ibid.

229. Ibid. p.30.

230. Ibid. pp.31-2.

231. Gleason (1922, 1925a).

232. Arrhenius (1921).

233. Gleason (1922), pp.158-9.

234. Gleason (1963-4) 1, pp.230-1.

235. Gleason (1925a), p.66.

236. Ibid. p.68.

237. Ibid. p.70.

238. Gleason (1944), pp.45-6.

239. Gleason (1925a), p.71.

240. Ibid.

241. Ibid.

242. Ibid. p.74.

243. Ashby (1936), pp.222-3.

244. Goodall's (1962) bibliography allows a comparison to be made between statistical activity in American and European ecology.

245. See Du Rietz (1921) and Raunkiaer (1934).

246. Forbes (1907).

247. Forbes (1925). See also, Calvert (1922).

248. Gleason (1963-4) 1, p.120.

249. Cronquist (1976), p.56.

250. Interview, A.M. Gleason.

251. Gleason (1963-4) 1, p.370.

252. I am grateful to Mr. G. Cohen for reading Gleason's statistical papers and for providing me with this assessment.

253. See, for instance, Greig-Smith (1957), p.IX.

254. See, for instance, Gleason (1936a), p.47. This article, in which Gleason reviewed the progress of ecology from 1910 to 1935, gives a clear indication of the importance he accorded his own work.

255. For the relation between orthodox and experimental taxonomy, see Dean (1979).

256. Goodall (1962), pp.294-6.

257. Gleason (1963-4) 1, p.371. See also, Woollett, Dean and Coburn (1925).

258. For empirical studies of the structuring of cognitive innovation around previously acquired skill, see Pickering (1980), and Mackenzie and Barnes (1975).

259. There was little emphasis on mathematics in the professional education of ecologists in the 1940s and 1950s, interviews, R.H. Whittaker and P. Greig-Smith.

260. Such a form of distribution is compatible with the individualistic hypothesis and apparently incompatible with the association-unit theory. It is not, however, required by the individualistic hypothesis that distribution be uniform or random. Since the development of niche theory, other individualistic theorists have held quite different views on this matter - see McIntosh (1975), p.257.

261. Gleason (1923b).

262. Gleason (1953), pp.40-1.

263. Ibid.

264. Adams (1902, 1905).

265. Cain (1944) p.185.f.

266. See the discussion of "Past climates and climaxes" in Clements (1916), pp.317-43.

267. Gleason (1907), p.57.

268. Sears (1969), p.128.

269. Raup (1942), p.331.

270. Shreve, et al. (1910), quoted in McIntosh (1983), p.110.

271. Cowles (1908), pp.265-6.

272. Ibid. pp.270-1.

273. Clements (1905), p.2, Clements (1908).

274. Gleason (1925b).

275. Gleason and Cook (1927).

276. Emerson (1939a).

277. Ibid. p.7.

278. Ibid.

279. Ibid. pp.9-10.

280. The technique of association identification by character species is described in the previous chapter.

281. Ibid. pp.10-11.

282. See Hewetson (1955) and Richards (1952).

283. Gleason (1926a), p.14.

284. Ibid.

285. Ibid. pp.21-22.

286. Ibid. p.17.

287. Ibid. pp.15-16.

288. Clements (1916), p.3.

289. Weaver and Clements (1938), p.6.

290. Letter, W.S. Cooper to Curtis, March 25th 1946. Curtis Papers.

291. Cain (1947), p.196.

292. Nichols (1923), p.13.

293. Gleason (1944), p.20.

294. Gleason (1923a).

295. Gleason (1936b). See Cain (1936).

296. Interview, H.A. Gleason Jnr.

297. Gleason (1963-4) 1, p.336.

298. See note 258 above. For a review of this literature see Shapin (1982).

299. Gleason (1944), p.28.

300. McIntosh (1983), p.110, Billings (1980).

301. Livingston and Shreve (1921), p.XIV.

302. Cooper (1926), p.394.

303. Shreve (1915), pp.111-2.

304. Livingston and Shreve (1921), p.5.

305. For biographical details of Shreve, see Shantz (1951).

306. Livingston (1948), p.232.

307. Ibid. pp. 233-4.

308. Livingston and Shreve (1921), p.XIV. This is an extension of a passage quoted from above, see footnote 301.

309. Ibid. p.10.

310. Livingston and Shreve admitted, however, that there were a few species which might not have the geographical limits of their distribution determined directly at any particular point in time by the intensity of some physical factor. Newly-evolved species, for example, might still be expanding their range and therefore not yet reached the limits of their physical tolerances.

311. Shreve (1915).

312. Livingston and Shreve (1921), p.21.

313. Shreve (1914), p.107.

314. Gleason (1927).

315. McIntosh (1983), p.110.

316. Nichols (1926).

317. Gleason (1926b).

318. Nichols (1926), p.630.

319. Ibid. p.631.

320. Ibid.

321. This tactic is discussed by Shapin (in preparation). I am grateful to Dr. Shapin for allowing me to consult and refer to an early version of his paper.

322. Nichols (1926), p.630.

323. Ibid. p.631.

324. Hall and Clements (1923).

325. Ibid. p.4, also Clements (1905) p.12.

326. Rydberg (1926), p.1540.

327. Gleason (1961), pp.44-5.

328. This episode and the continuation of this debate have been discussed in much greater detail by Dean (1980).

329. Sprugel (1980), p.199.

330. Nichols (1926), p.632.

331. Ibid.

332. Ibid. p.633.

333. Ibid. p.635.

334. For the notion of "producing a world" see Pickering (forthcoming).

335. For a discussion on how the distinction between "anomaly" and "crucial example" is paradigm-relative, see Kuhn (1962), pp.52-65.

336. Nichols (1926), p.639.

337. Gleason (1926b), p.643.

338. Ibid. p.644.

339. Ibid.

340. Interview, H.A. Gleason Jnr, see also Gleason (1938, 1952b, 1955) and the several "Taxonomic essays" in Gleason (1962), pp.11-74. Gleason was a conservative, non-splitting taxonomist.

341. Gleason (1926b), p.645.

342. Ibid. p.646.

343. Gleason (1963-4) 2, p.263.

344. Gleason (1953), p.42.

345. Letter, I. Johnston to Gleason, 25th March 1929, Gleason Papers.

346. Interview, F.E. Egler. Nichols was, however, well-known for speaking harshly to his students, Steere (1977), pp.330-1.

347. Gleason (1927).

348. Gleason (1929, 1936b).

349. Gleason (1963-4) 2, p.352.

350. Gleason (1933).

351. Gleason (1963-4) 2, p.361.

352. Ibid. p.353, Letter, Gleason to Oswald, 30th Sept. 1927, Gleason Papers.

353. See Pavillard (1935), p.218.

354. Lenoble to Gleason, 24th Aug. 1927, Gleason Papers.

355. Gleason (1961), p.3.

356. Letter, Gleason to M. Howe, Feb. 8th, 1928, Gleason Papers.

357. Letter, C. Hottes to Gleason, Jan. 11th, 1929, loc. cit.

358. Letter, C. Hottes to Gleason, April 9th, 1929, loc. cit.

359. Gleason (1963-4) 2, pp.302-3.

360. Ibid. 3, p.80.

361. Letter, Gleason to F.A. Loew, Jan. 7th, 1937, Gleason Papers.

362. Letter, Gleason to F. Eggleton, Dec. 17th, 1940, loc. cit.

363. Gleason (1963-4) 2, p.263.

364. Cain's relationship in the ecological establishment is discussed in more detail in the following chapter.

365. Cain (1947), p.198.

366. Cain (1944), p.XIV, (1947), p.197.

367. Gleason (1963-4) 2, p.263.

368. Letter, S.A. Cain to Gleason, Aug. 27th, 1937. Gleason Papers.

369. Letter, Gleason to Cain, Sept. 7th, 1939, loc. cit.

370. Cain (1939).

371. Letter, Cain to Gleason, Jan. 24th, 1938, Gleason Papers.

372. Gleason (1926, 1927).

373. Gleason (1939), p.107.

374. Letter, Cain to Gleason, Nov. 22nd, 1937, Gleason Papers.

375. See Worster (1977), pp.326-32.

376. Emerson (1939a).

377. Emerson (1939b), pp. 109-110.

378. Malin (1955), p.403.

379. Malin (1953), p.16.

380. Malin (1955), p.403.

381. Gleason (1922), p.41.

382. Interview, H.A. Gleason Jnr.

383. Gleason (1963-4) 2, pp.163-65.

384. As Bowers has pointed out (1974), the Country Life Movement, with its strong faith in agrarianism, gained much of its support from those members of the urban professional middle classes who were only a single generation from the farm.

385. Gleason (1963-4) 2, pp.165-6.

386. *Ibid*. p.171.

387. For urbanite agrarianism, see Schmidt (1969). For Jeffersonian agrarian individualism, see Peterson (1960).

388. There is much evidence of Gleason's attitude on these matters throughout his autobiography. My opinion is also supported by personal communications from two of Gleason's former colleagues - interviews, A. Cronquist and W.C. Steere.

389. Gleason (1963-4) 3, p.45.

390. *Ibid*. p.347 and throughout chapter 13.

391. Gleason (1952b), p.20.

392. See Gleason (1963-4) 2, pp.170-1 and p.362.

393. See Godwin, H. (1940).

394. Letter, Eggleton to Gleason, Dec. 17th, 1940, Gleason Papers.

395. Letter, Gleason to Eggleton, Dec. 20th, 1940, loc. cit.

396. Letter, Gleason to Eggleton, Dec. 23rd, 1947, loc. cit.

397. Letter, Gleason to Eggleton, Feb. 27th, 1942, loc. cit.

398. Interview, Frank E. Egler, Nov. 25th, 1978.

399. Gleason (1963-4) 2, p.264, interview, F.E. Egler.

400. Cain (1947), Egler (1947).

401. For a good discussion of the theoretical importance of this work, see McIntosh (1967).

402. Meyer (1956), p.17 - at the same ceremony, S.A. Cain, W.S. Cooper, E. Braun, D.T. MacDougal, E.N. Transeau, J.E. Weaver and H.S. Conard were all awarded certificates which cited their service to ecology. Gleason was the only ecologist honoured whose services to ecology were not mentioned.

403. J.T. Curtis to Gleason, Jan. 14th, 1955, Curtis Papers.

404. See, for example, Daubenmire (1966).

405. Cain (1959), p.106.

406. Interview, H.A. Gleason Jnr.

407. Gleason (1963-4) 2, p.264.

CHAPTER 4

1. For an account of the "individualistic dissent" as it occurred world-wide, see Whittaker (1962), pp.78-83.

2. Whittaker (1956), pp.40-3.

3. Mason (1947), Cain (1947), Egler (1947a).

4. The statement is borne out by the opinions of P. Greig-Smith, R. McIntosh, G. Cottam, R.H. Whittaker, interviews.

5. I describe some of these criticisms in chapter two. For an important example, not previously discussed, see Tansley (1935).

6. It is instructive to compare the fulsome and enthusiastic tributes paid to Cowles, both on his retirement, Cooper (1935), and after his death, Adam and Fuller (1940), with the generally diffident tone of the articles in the issue of Ecology. volume 35, #2, 1954, which was dedicated to Clements. However, that an issue was dedicated to Clements, albeit nine years after his death, is a mark of his stature.

7. Griggs (1934), p.154.

8. *Ibid*. p.174.

9. Raup (1941), pp.232-6. This paper is partially reprinted in Stout (1983). Stout's collection provides a good introduction to Raup's work.

10. Raup (1942), p.331.

11. Raup (1951, 1957); both these papers are partially reprinted in Stout (1983).

12. Stout (1983), p.131.

13. Raup (1942), p.347.

14. Interview, Sir Harry Godwin.

15. This episode is described in Gleason (1963-4) 1, pp.332-42.

16. *Ibid*. p.332.

17. *Ibid*. p.338.

18. *Ibid*.

19. Covington (1944).

20. Odum (1977).

21. For the expansion of professional opportunities for ecologists in the New Deal, see Swain (1963), chap. 9.

22. Richardson (1973). McConnell (1954) and Fleming (1972) are good for descriptions of the vicissitudes of the conservation movements. Flader (1974) contains much incidental information about the status of applied ecology and professional conservationists, especially chaps. 5 and 6.

23. Young (1954), p.116.

24. Letter, D.B. Lawrence to Curtis, 3 Aug. 1948, Curtis Papers.

25. Burgett (1977), p.3.

26. Cooper (1935), p.283.

27. For the shift of Rockfeller funds, see Weaver (1958), Beadle (1967) and Abir-Am (1982).

28. See Mullins (1972) for a description of one stage of the process. See Abir-Am (1982) for an interesting general analysis.

29. This account of the Carnegie Institute's involvement in ecology is taken from McIntosh (1983).

30. McIntosh (1983), p.110.

31. Clements's Lamarckianism is described by Tobey (1981), pp.85-87. Neo-Lamarckianism in American environmental science more generally is discussed by Sterling (1978). I am grateful to Prof. K.B. Sterling for providing me with a copy of this paper. See also Sterling (1977).

32. Letter, Clements to Merriam, President of the Carnegie Institution, Dec. 2, 1928, quoted in McIntosh (1983).

33. Dean (1979, 1980) has discussed the work of Clausen, Keck and Hiesey. An otherwise excellent treatment is marred by Dean constantly referring to Clausen _et al_. as "ecologists". This identification is erroneous, as is shown by the following quotation:-

    > "Do you remember Constance's remarks in _Ecology_ recently that the librarian at Berkeley who classified Clausen, Keck and Hiesey's work under ecology obviously hadn't been through any modern school of ecology..."

    Letter, J. Major to Curtis, Dec. 24 , 1942, Chrtis Papers.

    Clausen, Keck and Hiesey are better termed "genecologists". Referring to them as "ecologists" blurs an important professional distinction. They are members of a different specialty from Clements, Cooper, Nichols _et al_. Hence the rivalry between Clements and Clausen is not between plant ecologist and plant ecologist, but between an ecologist and a member of a more successful specialty.

34. Cain (1944), p.XIV.

35. See Allen (1978), Chap. 5.

36. Provine (1978), p.179. Provine continues "The same assertion could not have been made in 1925, or even in 1930".

37. Raup (1942), p.334. I have described the professional rivalry between ecology and floristic botany in the previous chapter.

38. Steere (1977), pp.330-332.

39. See Kevles (1978), pp.324-392.

40. On this matter the ecologists identified with biologists generally. W.A. Dayton (1948), representative to the Union of American Biological Societies reported to the E.S.A.:-

> "It has become increasingly apparent, especially with the onset of World War Two, that the biological sciences in this country are, in some respects, not on a parity with the physical sciences."

The ecologist, R.F. Griggs (1942, 1945, 1947) campaigned strongly for more prominence to be given to biological and environmental science in the national context.

41. For the background to the "ideology of national science", see Tobey (1971). The Ecological Society of America was greatly exercised, in the late forties and early fifties, to present ecology as a vital part of the nation's scientific endeavour:-

> "The National Security Resources Board is formulating a new national policy for the use of scientifically trained men to the best advantage of our military program and national life. This board has requested help in developing a policy for the National Research Council which in turn has contacted the Ecological Society and requested that a committee be appointed within our group to work with them."

Letter, Kendeigh to Curtis, Dec. 14, 1950, Curtis Papers.

The doings of this committee and the Committee for Cooperation with the National Research Council occupy many pages of the Bulletin of the Ecological Society of America between 1948 and 1955.

42. Curtis, refereeing Whittaker's application for a Guggenheim Fellowship wrote:-

"I might suggest that if a Fellowship be granted to him, he be urged to reconsider his choice of spending full time at Berkeley. The University of California is notorious among ecologists for its antediluvian ideas about ecology. What Whittaker needs most is the advice and counsel of other ecologists who have actually practised ecology."

Letter, Curtis to the Guggenheim Foundation, Jan. 31, 1955, Curtis Papers.

43. I am grateful to Dr. Arthur Cronquist and Dr. Frank Egler for supplying me with information about Herbert Mason and his students.

44. Mason (1947), p.203-4.

45. Ibid. p.203.

46. Ibid. p.205.

47. Ibid. p.210.

48. Ibid. p.204. It should be noted that incompatibility between the Neo-Darwinian theory and the community-unit theory is not a priori necessary. Different plant species might grow together because they had, by natural selection, become adapted to each other's presence, Harper (1967), p.208; Goodall (1966). Community-units might represent co-evolved groups of species. Thus it was potentially possible for the community-unity theorist as well as the individualistic theorist to justify his position in Darwinian terms. As a matter of fact, however, only the individualistic theorists did this. The American traditionalist ecologists chose to justify their practice in traditional terms.

49. Mason (1947), p.204.

50. Ibid.

51. John L. Harper (1967), for example, interview, R. McIntosh.

52. These aspects of Gleason's statistical work are discussed in the previous chapter.

53. Cain (1947), p.189.

54. Ibid. p.197.

55. Ibid. p.188.

56. Ibid. p.195.

57. Ibid. p.189.

58. Ibid. p.196.

59. Ibid. p.198

60. Burgess (1977), p.7.

61. Cain (1936).

62. Cain and Castro (1959).

63. Letter, Fuller to Gleason, Jan. 20, 1936, Gleason Papers.

64. Interview, F.E. Egler.

65. Ibid. The fact that these three articles were being written independently at approximately the same time tells us much about the underlying state of the discipline of ecology. Simultaneous and yet independent events are quite common in the history of science. The most dramatic of such events, simultaneous and independent discoveries, have attracted much scholarly attention. Merton (1973), Chaps. 16 and 17, see also Brannigan (1982), Chap. 4, for a less normative interpretation.

    In all the cases so far studied, the independence of the discoveries might be said to be more apparent than real - in the sense that each of the individual actors responds to similar supra-individual pressures and trends. Simultaneous discoveries well exhibit the essentially social location of scientific research. In the present case, the startlingly synchronous appearance of fresh support of Gleason from three independent authors vindicates the seeking of explanations for the revival of the individualistic hypothesis within the social circumstances of plant ecology as a discipline in the nineteen-forties. The stresses the discipline as a whole was being subjected to encouraged theoretical reassessment simultaneously by several, ostensibly independent, individuals.

66. Interview, F.E. Egler.

67. Egler (1947a).

68. Ibid. p.388.

69. Ibid. p.389.

70. Ibid.

71. Ibid.

72. Ibid.

73. Interview, F.E. Egler.

74. Daubenmire (1947), Oosting (1948). These books were both quite closely based on lecture courses given by W.S. Cooper, interviews, A. Cronquist, F.E. Egler.

75. Daubenmire's book was principally devoted to autecology. Only by implication did it contain the position on communities I have here described. However, such a position is explicit in Daubenmire's research articles of the same period, see Daubenmire (1943, 1952).

76. McDougall (1949), p.III.

77. Egler (1951), p.676.

78. Ibid. pp. 677-8. As well as the three books mentioned in the main text, Egler (1951) also reviewed Allred and Clement (1949) - a selection of F.E. Clements' writings.

79. Ibid. p.675.

80. Ibid. p.685.

81. Interview, F.E. Egler.

82. Egler (1951), p.686, emphasis in the original.

83. I am grateful to the graduate seminar, Ecology Division, Cornell University for biographical information on Oosting and Daubenmire.

84. This must be regarded as a provisional statement. My only source for it has been a thorough scrutiny of their published works.

85. Interview, F.E. Egler.

86. See, for example, Daubenmire (1942, 1943, 1952, 1956).

87. Interview, F.E. Egler.

88. Ibid. See also Egler (1947b). The 1951 paper was intended by Egler to be his farewell to ecology. He had come to see the field as unreformable. Also an eye disorder threatened his career in research, interview, F.E. Egler.

89. Interviews, R.P. McIntosh, A. Cronquist; Letter, Cain to Curtis, Sept. 22, 1952, Curtis Papers.

90. Interview, F.E. Egler.

91. Egler (1960), p.236.

92. Interview, R.H. Whittaker.

93. _Ibid_.

94. Interviews, R.H. Whittaker, H.A. Gleason, Jnr.

95. Interview, R.H. Whittaker.

96. Random sampling had by this time become accepted by statisticians as the best means of obtaining unbiased data (Pers. comm. Mr. G. Cohen). Placing plots at random in a large stand of vegetation is, however, extremely difficult and time-consuming - involving much surveying. Whittaker was vague both in his thesis and in our conversation as to how exactly he located his sample plots. It is likely that his sampling method was not strictly a random one. The important novel aspect of his methodology was that he did not locate his sampling sites according to an _a priori_ assumption as to what the vegetation types were. Whittaker was employing, if somewhat rhetorically, criteria of objectivity derived from the more prestigious discipline of statistics.

97. Whittaker (1948), p.1.

98. Interview, R.H. Whittaker.

99. _Ibid_.

100. _Ibid_.

101. _Ibid_.

102. Whittaker (1948), p.144.

103. Interview, R.H. Whittaker.

104. Whittaker (1948), p.144.

105. It is a sign of the ubiquitous presentation of quantification as the mark of good science that a graduate student with no special training in mathematics should choose to devise new quantitative techniques. This example demonstrates that, important though prior training is as an explanation of scientists' behaviour , it is not always a complete explanation. Actors may decide that it would be advantageous to gain new skills.

106. _Ibid_. p.147.

107. Interview, R.H. Whittaker.

108. _Ibid_.

109. _Ibid_.

110. _Ibid_.

111. See Whittaker (1948), p.123.

112. See Camp (1951).

113. The rise of biosystematics has been discussed by Dean (1980).

114. See Camp (1931).

115. Gleason (1962), p.III acknowledged that his views on the species concept had been developed by his discussions with Camp. There is considerable correspondence between the two men in the Gleason Papers.

116. Letter, Whittaker to Gleason, June 2, 1949.

117. Letter, Curtis to Whittaker, June 2, 1954; interview, R.H. Whittaker.

118. Whittaker (1956). However, Whittaker had, by this time, published the insect studies he had done in the Great Smokies (1952), and two theoretical articles dealing with the questions of association and climax (1951, 1953). The arguments in the theoretical articles were substantiated by Great Smoky material.

119. Interview, R.H. Whittaker.

120. Ibid.

121. Ibid.

122. Biographical details of Curtis are, except where indicated, extracted from several curricula vitae in the Curtis Papers. I have drawn in particular from his two Guggenheim applications, 1942 and 1955, and the career outline he supplied to the ecology seminar, Rutgers University, letter, Curtis to W.E. Martin, Jan. 8, 1958, Curtis Papers.

123. Interview, G. Cottam.

124. Curtis (1932a,b; 1933).

125. Such early competences are seen in many of the ecologists I have discussed. Gleason is an outstanding example. They form part of the pattern of successful recruitment to the profession.

126. For Duggar, see Walker (1958).

127. Hollaender and Curtis (1935).

128. See Walker (1958).

129. For a good description of this work, see Frey (1963), pp.3-54.

130. Curtis and Juday (1937).

131. Frey (1963), p.40.

132. I have elsewhere considered why Curtis, in mid-career, abandoned physiology and became an ecologist, Nicolson (1981).

133. For Leopold, see Flader (1974).

134. Letter, Curtis to Greig-Smith, Feb. 10, 1958, Curtis Papers.

135. Letter, Curtis to Oosting, Aug. 6, 1959, Curtis Papers.

136. This was published as Curtis (1947).

137. Holdridge was then with the Forestry Division of the Société Haitiano-Americaine de Developpement Agricole. The Emergency rubber project also came under the auspices of this organisation.

138. Letter, Curtis to Cooper, March 12, 1946, Curtis Papers.

139. Letter, Curtis to W.E. Martin, Jan. 8, 1958, Curtis Papers.

140. Interview, G. Cottam; Letter, Curtis to W.E. Martin, Jan. 21, 1958, Curtis Papers.

141. Letter, Curtis to P. Greig-Smith, Feb. 10, 1958, Curtis Papers.

142. Cottam and Curtis (1949).

143. Interview, G. Cottam.

144. Curtis and Greene (1948); Curtis and McIntosh (1950).

145. Cottam and Curtis (1948).

146. Letter, Curtis to D.B. Lawrence, Oct. 13, 1947. Curtis Papers.

147. Curtis and Partch (1948).

148. Curtis received several letters from editors congratulating him on the excellent quality of his submissions, for example, D.B. Lawrence to Curtis, April 17, 1950, Curtis Papers.

149. Interview, G. Cottam.

150. Letter, Curtis to R.H. Whittaker, Feb. 6, 1960, Curtis Papers.

151. Letter, Curtis to H.J. Oosting, Aug. 6, 1959, Curtis Papers.

152. Interview, R.P. McIntosh.

153. Ibid.

154. Whitford, one of Curtis's first students had produced a classification of the southern hardwoods of Wisconsin, Whitford (1949). Curtis saw this as heuristically useful but only a first approximation; interview, R.P. McIntosh.

155. Interview, R.P. McIntosh.

156. Curtis and McIntosh did however describe their selection of stands as "essentially random", Curtis and McIntosh (1951), p.480. As I have argued above, note 92, this was a reference to culturally given standards of objectivity.

157. It is now the opinion of ecologists that unless a sampling technique is predicated upon a system of classification, the resulting data will not fall into distinct groupings, interviews, R.H. Whittaker, P. Greig-Smith, R.P. McIntosh.

158. The claim in Curtis and McIntosh (1951), p.478 that one of the aims of the study was "to determine whether discrete communities with definite structure and definable boundaries actually exist" was, at least partly, a *post hoc* reconstruction; interview, R.P. McIntosh.

159. Interview, R.P. McIntosh. Cottam, who shared an office with Curtis for some of this period, recalls that attempts at organising McIntosh's data took many months; interview, G. Cottam.

160. McIntosh and Curtis (1950).

161. Letter, Whittaker to Curtis, Sept. 15, 1950, Curtis Papers.

162. Interview, G. Cottam.

163. Curtis and McIntosh (1951).

164. See *Bull.Ecol.Soc.Amer*. (1951), *32*, pp.56-57 for abstracts of the papers given at the Minneapolis meeting.

165. Letter, Curtis to F.E. Egler, Nov. 13, 1951, Curtis Papers.

166. Interview, G. Cottam.

167. Curtis and McIntosh (1951), p.488.

168. *Ibid*. p.486.

169. Letter, Lawrence to Curtis, March 25, 1951, Curtis Papers.

170. It is worth noting that a Clementsian could have replied to Whittaker that the vegetation of the Great Smoky Mountains was not uniformly genuine climax. Only after erosion had leveled the mountains would a genuine climax vegetation be established. Therefore, whether or not Whittaker's data counted as a refutation of Clementsian theory depended on

a paradigm-dependent definition of climax. Most ecologists would however have accepted the vegetation of the Smokies as climax over most of its area, and therefore they criticised Whittaker on the question of sampling.

171. Letter, Curtis to W.H. Camp, July 6, 1949, Curtis Papers.

172. Letter, Curtis to C.G. van Steenis, Oct. 8, 1956, Curtis Papers.

173. Curtis (1955), p.565.

174. Letter, Cain to Curtis, Sept. 22, 1952, Curtis Papers.

175. With the proviso that in Whittaker's case a gradient was first chosen and samples taken along it, e.g. down the slope of a hillside, whereas in Curtis's case, the first step was to sample vegetation. The samples were arranged into a continuum by floristic criteria. The environmental bases for such distribution were sought secondarily. In the Tennessee example, the gradients were obvious; in Wisconsin they were not.

176. Letter, Cain to Curtis, Sept. 26, 1952, Curtis Papers.

177. Some of this work is to be found in the following: Brown and Curtis (1952), Gilbert and Curtis (1953), Hale (1955), and Tresner, Backus and Curtis (1954).

178. Eventually published as Bond (1957).

179. p.12, "The continuum in relation to the classification of plant communities" - a talk presented to the A.A.A.S. symposium Dec. 30, 1952, St. Louis, unpublished typescript in the Curtis Papers.

180. Interview, G. Cottam.

181. Letter, Curtis to W.E. Martin, Jan. 8, 1958, Curtis Papers.

182. Letter, Curtis to C.G. van Steenis, Oct. 8, 1956, Curtis Papers.

183. Letter, Curtis to R.P. McIntosh, Nov. 6, 1952, in the possession of R.P. McIntosh.

184. Letter, Curtis to Goodall, Nov. 7, 1952. Goodall (1952), Hewetson (1956). For a survey of changing views on the tropical rain forest, see Richards (1952).

185. Letter, Cain to Curtis, Sept. 22, 1952, Curtis Papers.

186. Letter, Curtis to H.A. Gleason, Jan. 14, 1955, Curtis Papers.

187. Letter, Curtis to G. Cottam, Sept. 14, 1954, see Bray and Curtis (1957).

188. Curtis (1959).

189. Garfield (1975). I am indebted to R.P. McIntosh for this reference. Garfield does not claim that this list is wholly accurate or complete. There were only 11 ecology papers in the 101 - most of the others being from plant genetics, physiology or biochemistry.

190. Curtis and McIntosh (1951), Bray and Curtis (1957). The third was Cottam and Curtis (1956).

191. Letter, Curtis to R.P. McIntosh, April 8, 1959, in the possession of R.P. McIntosh.

192. Daubenmire (1960, 1966). See also Langford and Buell (1969). However a search in the Science Citation Index revealed that neither of these papers was extensively cited between 1970 and 1978. Daubenmire was cited 15 times, Langford and Buell, 19. The majority of the citing papers were hostile. Although Daubenmire remained resolute for the community-unit, Oosting was eventually converted to gradient analysis, Mowbray and Oosting (1968), and paid a generous tribute to Whittaker, p.309.

193. Interviews, R.H. Whittaker, P. Greig-Smith. This is only true of the English-speaking world. European phytosociology is more quantitative than it was but, generally speaking, is still based on community-unit, as described in Chapter 2.

194. This example may at first seem to support Mulkay's claim that middle-status scientists are the "least likely to deviate from group opinion or group norms" (1972, p.48). Note, however, that it is not their status per se which conditions Daubenmire's and Oosting's response to innovation, but the degree of their commitment to the status quo. I would argue that they were "reformers" rather than "revolutionaries" because they did not possess expertise outside the traditional framework of ecological research.

195. It is interesting to note that the Wisconsin school possessed almost all the characteristics which Morrell (1972) posited in his "conjectural model of an ideal research school". viz., charismatic leader, leader with research reputation, informal setting and leadership style, leader with institutional power, esprit de corps and discipleship, focused research programme, new, simple and rapidly exploitable research techniques, pool of recruits (graduate students), access to publication outlets, students publish early under own names, produced and "placed" significant number of students (most of

Curtis's early students gained academic positions), institutionalisation in a university setting, and adequate financial support. For a discussion of other criteria, see Edge and Mulkay (1976), pp.364-86; for a general discussion of the phenomenon of emerging research schools, see Geison (1981).

196. I am not suggesting that R.H. Whittaker's work was not eventually recognised nor that his career was blighted. He became a very eminent ecologist. The Wisconsin work on the continuum was however accepted more quickly and cited more frequently.

CONCLUSIONS

1. Tobey (1981).

2. Ibid. p.204.

3. Sprugel (1980), p.199.

4. Ibid.

5. Burgess (1977), p.7. The Wisconsin school were, in the fifties, well aware of the continued dominance of the Chicagoans, interview, G. Cottam.

6. Tobey (1981), p.223.

7. Egler (1951), p.671, wrote:-

   "Henry C. Cowles wrote relatively little, devoting his energies mainly to the training and development of his graduate students, through whom he still speaks".

8. Ibid. p.68.

9. Ibid. p.69.

10. See Simberloff (1980) for a description of Clementsian ecology as essentialist.

11. Pound and Clements (1898b).

12. An ecotone is an area of transition between two formations or associations.

13. Tobey (1981), p.111.

14. Ibid. p.7.

15. Ibid. pp.170-171.

16. Ibid. p.175.

17. For a historical description of the New Ecology, see McIntosh (1974), pp.138-48; for the historical development of the emphasis on energy flow and energy budgets, see E.P. Odum (1968). See Cook (1977) for a study of one of the pioneers of the New Ecology.

18. See Gates (1968) and McIntosh (1974). For a descriptive history of system theory and an interesting sociological analysis, see Lilienfeld (1978).

19. See McIntosh (1974), pp.133-5.

20. This point is made strongly by Worster (1978), p.311.

21. This has been noted by Simberloff (1980), p.5.

22. E.P. Odum (1977), p.1289.

23. *Ibid.* p. 1290.

24. H.T. Odum and Pinkerton (1955).

25. H.T. Odum (1957), p.108.

26. Letter, Curtis to H.J. Oosting, Feb. 10th, 1961, Curtis Papers. Curtis was refereeing one of H.T. Odum's papers for *Ecological Monographs*.

27. Leeper (1977) provides an informative profile of E.P. Odum and his present status.

28. E.P. Odum (1977), p.1290.

29. *Ibid.* p.1291. The Odums have produced many such statements, for example, see also H.T. Odum (1977).

30. Lowe and Warboys (1980), p.441.

31. See McIntosh (1980), pp.239-44 for a short description of this controversy and its personnel.

32. Harper (1977), p.777.

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