Evolution Under Our Feet

Anthony David Bradshaw (1926–2008) and the Rise of Ecological Genetics

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ABSTRACT

How fast is evolution? In this dissertation I document a profound change that occurred

around the middle of the 20th century in the way that ecologists conceptualized the temporal

and spatial scales of adaptive evolution, through the lens of British plant ecologist Anthony

David Bradshaw (1926–2008). In the early 1960s, one prominent ecologist distinguished

what he called "ecological time"—around ten generations—from "evolutionary time"—

around half of a million years. For most ecologists working in the first half of the 20th

century, evolution by natural selection was indeed a slow and plodding process, tangible in

its products but not in its processes, and inconsequential for explaining most ecological

phenomena. During the 1960s, however, many ecologists began to see evolution as

potentially rapid and observable. Natural selection moved from the distant past—a remote

explanans for both extant biological diversity and paleontological phenomena—to a

measurable, quantifiable mechanism molding populations in real time.

The idea that adaptive evolution could be rapid and highly localized was a significant

enabling condition for the emergence of ecological genetics in the second half of the 20th

century. Most of what historians know about that conceptual shift and the rise of ecological

genetics centers on the work of Oxford zoologist E. B. Ford and his students on

polymorphism in Lepidotera, especially industrial melanism in *Biston betularia*. I argue that

ecological genetics in Britain was not the brainchild of an infamous patriarch (Ford), but

rather the outgrowth of a long tradition of pastureland research at plant breeding stations in

Scotland and Wales, part of a discipline known as "genecology" or "experimental

taxonomy." Bradshaw's investigative activities between 1948 and 1968 were an outgrowth of

the specific brand of plant genecology practiced at the Welsh and Scottish Plant Breeding

stations. Bradshaw generated evidence that plant populations with negligible reproductive

isolation—separated by just a few meters—could diverge and adapt to contrasting environmental conditions in just a few generations. In Bradshaw's research one can observe the crystallization of a new concept of rapid adaptive evolution, and the methodological and conceptual transformation of genecology into ecological genetics.

ACKNOWLEDGMENTS

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INTRODUCTION

In the autumn of 1948 a young plant ecologist named Anthony David Bradshaw arrived at the Welsh Plant Breeding Station at Aberystwyth, in western Wales, to commence his Ph.D. research. In an essay about plant communities that he wrote shortly after his arrival, Bradshaw asserted that, "man has only exercised influence on the vegetation for the last six thousand years, which gives little chance for the bulk of the vegetation to evolve in relation to those effects" (D1041/1/11/87). Evolution was not inconsequential for explaining the patterns of plant distribution and association in the British landscape, but for Bradshaw it was slow and plodding, involving small, incremental changes over thousands of years.

By the 1960s, however, Bradshaw's views had shifted radically. "We are brought up to think that the time scale of evolution is millennia," he wrote; "This may be true for the history of life, but it is not true for the immediate process of evolution within species" (Bradshaw 1965). In a presentation to the British Ecological Society in 1968, Bradshaw asserted that, "even twenty five years grossly over estimates the time needed" for the evolution of particular phenotypic traits (D1041/1/11). Between 1948 and the middle of the 1960s, Bradshaw developed a research program centered on patterns and processes of genetic differentiation within species of pastureland grasses and other herbage plants. By the 1960s, Bradshaw was convinced that populations of plants separated by even a few meters could diverge and adapt to contrasting environments in mere decades, or less. Natural selection moved from the distant past—a remote explanandum for extant species and varieties—to a measurable, observable mechanism molding plant populations in real time.

In the decades leading up to Bradshaw's research on pastureland grasses, natural selection had already moved to the foreground as a first-class explanation for evolutionary phenomena. The marriage of Mendelian genetics and Darwinism at the turn of the 20th

Figure I.1. Anthony David Bradshaw (1926–2008). Courtesy of the University of Liverpool Sydney Jones Library Special Collections & Archives.

century led to work by J. B. S. Haldane, Sergei Chetverikov, Sewall Wright, and R. A. Fisher in the 1920s and '30s that provided a mathematical formalization of evolutionary theory in terms of selection coefficients, population sizes, and gene frequencies (Provine 1971, 1989). By the end of the 1940s, the concept of a Modern Synthesis (Huxley 1942) in biology had crystalized around the idea, propounded by a few key "architects,"[1] that natural selection acting gradually on small variations in Mendelian populations was the primary cause of organic evolution (Mayr & Provine 1980, Smocovitis 1996, 1997, 2001, Kleinman 2012).

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[1] Including geneticist Theodosius Dobzhansky, ornithologist Ernst Mayr, paleontologist G. G. Simpson, and botanist G. Ledyard Stebbins

The Modern Synthesis conception of evolution by natural selection was strongly committed to gradualism, partly as a reaction against late 19th-century saltationist theories of evolution. Although early theoretical population genetic models did not strictly entail long time-scales, the explanatory aims of those models centered primarily on long-term evolutionary processes (the emergence of amphibians from early lungfish, for example) that could be observed in the fossil record (Roughgarden 1979; p. 5). Fisher and Haldane's models generally assumed that selection coefficients were extremely small, entailing a time-span of hundreds of generations for a new allele to go to fixation. Ecologist Lawrence Slobodkin captured the gradualist perspective by drawing a distinction between "ecological time"—around ten generations—and "evolutionary time"—around half a million years (Slobodkin 1961).

Bradshaw's transformation over the first two decades of his scientific career was a microcosm of a profound shift in the way that ecologists thought about the temporal and spatial scales of evolutionary change. The distinction between evolutionary and ecological time began to collapse in the middle of the 1950s, and the 1960s saw a surge of interest among population ecologists in natural selection (Collins 1986). If populations could evolve rapidly and locally enough to be observed over the course of a few years, then evolutionary changes could have a potentially profound impact on ecological processes. The strong selective pressures involved in those rapid changes meant that differentiation between populations could occur over very short distances, and Bradshaw's work demonstrated that this was so despite the potential for substantial gene flow.

By the end of the 1960s it seemed that a new field at the interface of evolution and ecology was taking shape. In 1968, theoretical ecologist Richard Levins observed that, "Contemporary population biology has emerged in the last few years as a result of the

convergence of the previously distinct disciplines of population ecology, biogeography, and evolutionary studies" (Levins 1968, p. 3). Levins credited that convergence to "increasing evidence ... that evolutionary, population genetic, biogeographic, and demographic events are not on entirely incommensurate time scales" and specifically that "natural selection has been observed in many cases to be strong enough to maintain differences between adjacent populations only meters apart in the face of high migration rates" (Levins 1968, p. 4). In an influential 1979 textbook, *Theory of Population Genetics and Evolutionary Ecology: An Introduction*, Jonathan Roughgarden noted a recent "union of population genetic theory with the theory of population ecology," called "evolutionary population ecology" (Roughgarden 1979, p. vii). Indeed, Roughgarden framed the book by discussing the evidence for, and implications of, rapid and local evolution (Roughgarden 1979, chapter 0). Unsurprisingly, Bradshaw's work was among the handful of cited examples.

The reality of rapid evolution implied that evolutionary models from theoretical population genetics could be more readily applied to empirical studies of natural populations. One of the hallmarks of Levins' and Roughgarden's "population biology" or "evolutionary ecology" was the possibility of studying the parameters of those models— such as selection and gene flow—in natural populations on ecologically relevant temporal and spatial scales. That was an approach that, by the mid-1960s, Bradshaw and his collaborators exemplified.

These changing ideas about the temporal and spatial scales of evolutionary change occurred during a period of a broader and equally radical transformation in understanding the relationships between human activities and environmental processes. Rising public concern over nuclear radiation, pesticide use, and overpopulation in the 1950s and 1960s stimulated new visions of the connectivity, vulnerability, and finiteness of the global

environment (Kline 2011). This led not only to the emergence of an increasingly vocal international environmental movement, but also to the re-articulation of ecological research as—in part—a critique of human impacts on the natural world (Kingsland 2008). At the same time, ecologists sought to create a more rigorous, quantitative, and predictive theoretical framework for studying ecosystem processes, and increasingly employed mathematical equations and computational models in their research (Kingsland 1995, Hagen 1992).

Why did Bradshaw change his mind about the temporal and spatial scales of adaptive evolution? How did he come to see natural selection as such as a powerful and pervasive agent of change in natural populations? According to Hooper (2002) and Collins (1986), part of what was truly groundbreaking in the 1950s and '60s was new evidence of rapid evolution taking place in natural populations. In December, 1955, zoologist E. B. Ford convened a meeting at the University Museum at Oxford to discuss the current state of research on evolution in natural populations. The meeting was predicated on "the realization that, in certain conditions evolution takes place in natural populations much more rapidly than had previously been suspected" (Ford 1956a, p. 291). Ford attributed that realization to an accumulation of new evidence about the genetics of natural populations produced through "a combination of laboratory genetics and ecological field work," that Ford called "ecological genetics" (Ford 1956a, p. 292).

Oxford is widely considered the birthplace of ecological genetics, and Ford its patriarch. Ford studied under zoologist Julian Huxley at Oxford in the 1920s, and returned to the University as a lecturer in the early 1940s (Hooper 2002). In his widely influential 1964 book, *Ecological Genetics*, Ford described ecological genetics in terms of both its methods and its epistemic aims:

The term "ecological genetics," which describes the technique of combined

field and laboratory work outlined here, has recently come into general use. I

have, however, for many years employed it in lectures and scientific

discussions, in which it has proved self-explanatory. Ecology, which denotes

the inter-relation of organisms with one another and with the environment in

which they live, may be regarded as scientific natural history. Consequently,

ecological genetics deals with the adjustments and adaptations of wild

populations to their environment. [...] Indeed it supplies the means, and the

only direct means, of investigating the actual process of evolution taking

place at the present time. (Ford 1964b, p. 53)

The work of one of Ford's students, H. D. B. Kettlewell, on industrial melanism in peppered

moths (Figure 2) remains among the iconic (albeit fraught) textbook examples of rapid

adaptive evolution. Work by Ford's students Philip M. Sheppard and Arthur J. Cain on

small-scale patterns of polymorphism in the banded snail *Cepaea nemoralis* was also widely

discussed at the time (Millstein 2008, 2009). Those and other studies helped to solidify the

identity of the "Oxford School of Ecological Genetics" (Rudge 2006). Kettlewell's melanic

Figure I.2. Melanic morphs of *Biston betularia*, the peppered moth. Picture taken by Olaf
Leillinger [http://de.wikipedia.org/wiki/Benutzer:Olei]. License: CC-BY-SA-2.5 and GNU
FDL.

moths remain the most widely known example of rapid evolution from the mid-20th century.

It is tempting to see Bradshaw's research and ideas as an outgrowth of Ford's ecological genetics, spillover from animal population ecology at Oxford into the plant ecology of British agricultural research institutions. But in this dissertation I will assess an alternate thesis: that the Oxford school was just one of multiple research traditions that directly contributed to the emergence of ecological genetics in the middle of the 20th century, and that catalyzed a reconceptualization of the temporal and spatial scales of adaptive evolution. One of those traditions was the agro-ecological field of genecology. Starting in the late 1910s, genecologists used a combination of field and laboratory techniques to study the relationships between hereditary variation within plant species and the various environmental conditions in which those species were found. As I shall describe, Bradshaw's research and ideas were a direct outgrowth of the British genecological tradition, which had little (if anything) to do with Ford and the Oxford school. Indeed, it is no accident that the most prominent organization for ecological genetics in Britain today, the Ecological Genetics Group, traces its heritage not to the zoologists of Oxford, but rather to a small group of plant breeders and agricultural plant ecologists—Bradshaw among them— in the middle of the 1950s (Peirson 2013).

This dissertation tells the story of Bradshaw's change of mind. But as I seek to illustrate, that change of mind should be seen as a facet of a far more complex transformation in Bradshaw's research. The acquisition of evidence for rapid evolution was not merely a matter of accumulating more data. Rather, it involved a reconfiguration of materials, practices, and modes of asking and answering questions—a change in the epistemic packaging that turned measurements of plant characteristics in the laboratory,

greenhouse, and field into evidence for evolutionary processes in nature. The transformations in Bradshaw's investigative pathway are analogous to the development of what Hans-Jörg Rheinberger (1997) has called an "experimental system." According to Rheinberger, scientific novelty is generated in part by the development and stabilization of particular configurations of material, procedural, institutional, and epistemic components that facilitate the asking and answering of specific kinds of questions. The notion of experimental systems is a recurring heuristic throughout this dissertation, as I follow the transformation of field and laboratory studies of intraspecific habitat-types into experimental studies of evolution in action through the lens of Bradshaw's research.

The proximate aim of this dissertation is therefore to document the changing practices, theoretical frameworks, and material contexts that both buttressed and comprised Bradshaw's early research, and that transformed adaptive evolution from a slow, historical process to a rapid, ongoing, and measurable one. I describe the research tradition into which Bradshaw was initiated, the community of scientists in which he worked, and the development of his investigative pathway over the next two decades. Using a computational analysis of the genecological research literature, I will also explore some of the consequences of his research program for the practice of ecological genetics and evolutionary ecology in the years after Bradshaw's change of mind. In so doing, this dissertation introduces a new cast of characters to the history of ecological genetics, and uses those characters as a window into the conceptual and methodological transformations in evolutionary ecology around the middle of the 20th century. The story of Bradshaw's change of mind is, in part, the story of how genecology contributed to ecological genetics.

This dissertation is not the first account of the history of genecology, experimental taxonomy, or biosystematics. Most of what we know about genecology centers on the work

of American experimental taxonomy and biosystematics. Joel Hagen and Betty Smocovitis have described the work of Swedish botanist Göte Turresson in the early 1920s, and his articulation of "genecology." Hagen has described the efforts of Frederic Clements and H. M. Hall at the Carnegie Institution of Washington to establish an "experimental taxonomy" that would legitimize ecological investigations of evolutionary phenomena (Hagen 1984). The extension of that project by Clements' successors, Jens Clausen, Keck, and Hiesey, was also extremely influential (Smocovitis 1988). Kim Kleinman has described the development of biosystematics in the midwestern United States, focusing on the work of Wendell Camp, Charles Gilly, and Edgar Anderson (Kleinman 2009). Most of that literature focuses on the impact of population thinking on the practice of taxonomy and systematics. But as Hagen (1984) notes, the epistemic aims of genecologists were quite diverse, and the research practices of those with less taxonomic interests remain under-documented.

Chapter 1 tells the story of Bradshaw's initiation into plant ecology, and into a particular style of genecological research. The purpose of this chapter is to provide the intellectual and material backdrop for the transformations that occurred during the 1950s and 1960s. I first describe Bradshaw's early training in ecology at The University of Cambridge. At the end of Bradshaw's undergraduate studies he encountered James W. Gregor at the Scottish Plant Breeding Station, who helped him to formulate a graduate research program focused on genecological problems. Indeed, although Gregor was not formally Bradshaw's graduate supervisor, he was unquestionably Bradshaw's foremost mentor during the formative stages of the younger ecologist's career. I describe the development of Gregor's own approach to genecology, starting in the 1920s, and characterize the research style—the epistemic aims, experimental methods, and theoretical framework—exhibited by Gregor in the decades leading up to his exchanges with Bradshaw.

Finally, I describe the early stages of Bradshaw's graduate research, and his initiation into the community of genecologists who worked at the Welsh Plant Breeding Station. This discussion highlights the deep entanglement of British agricultural development and genecology during the first half of the 20th century.

Chapter 1 sets the stage for the conceptual and methodological transformations that occurred in Bradshaw's work during the 1950s and 1960s. Göte Turesson's genecology provided a way of looking at variation in plants that struck a balance between the taxonomic interests of the 19th century and the new implications of 20th century genetics. The centerpiece of Turesson's theory was the "ecotype," a distinct form of a particular species specially adapted to a specific type of habitat. A crucial aspect of Gregor's approach to genecology, motivated by his work on *Plantago maritima* in Britain and Europe, was a gradual move away from attempts to delimit discrete intraspecific ecotypes. Instead, Gregor focused on characterizing patterns of heritable variation in specific phenotypic traits in relation to particular environmental gradients. As Gregor sampled on smaller spatial scales, it became clear that conceptualizing intraspecific variation in terms of separable and coherent types masked significant underlying causes of that variation. Gregor's method of sampling on small spatial scales, coupled with his interest in the causal linkage between specific environmental factors and differentiation in specific phenotypic traits, was a crucial starting-point for Bradshaw. Meanwhile, R. George Stapledon's interpretation of genecology as an agricultural research program at the Welsh Plant Breeding Station, starting in the 1910s, influenced Bradshaw's methodology and his choice of focal plant species. Those choices had significant consequences for how Bradshaw thought about local adaptive differentiation in plants.

In Chapter 2, I provide a detailed reconstruction of Bradshaw's investigative pathway between the commencement of his graduate studies in 1948 and his acceptance of the Chair of Botany at Liverpool in 1968. Bradshaw's early genecological research grew into a substantial research program centered on micro-geographic adaptation and mineral nutrition in pastureland grasses and other herbage plants. Bradshaw's research program transformed the agro-genecological tradition practiced by Gregor and Stapledon into a new science of plant ecological genetics. As I describe, Bradshaw's change of mind about the speed and locality of adaptive evolution was characterized not merely by a conceptual change, but rather by a shift in the aims and strategies of eco-evolutionary research. This shift involved a new set of questions, methods, and epistemic norms.

Bradshaw's change of mind about the temporal and spatial scales of adaptive evolution, combined with the genecological epistemic framework in which he was trained, also generated new ways of thinking about the relationship between evolutionary dynamics and developmental responses to the environment. In 1965, Bradshaw published what is now among the most influential works on the evolution of phenotypic plasticity. In Chapter 3, I place Bradshaw's ideas about plasticity in the context of his broader research program. I argue that his model of adaptive phenotypic plasticity should be seen as a reformulation of a long-standing debate in developmental genetics focused on organismal stability into a question about the adaptive relationship between specific traits and specific environmental factors in a genecological framework. This chapter has already been published in *Studies in the History and Philosophy of Science, Part C: Biological and Biomedical Sciences* as part of a special section on phenotypic plasticity in 20th-century plant sciences.

In chapter 4, I consider the development of plant ecological genetics in Britain through the lens of the Ecological Genetics Group. The EGG emerged in 1956 as an

informal gathering of genecologists and plant breeders from the Welsh and Scottish Plant Breeding Stations, nucleated by Bradshaw and Gregor. Over the next few decades the EGG diversified in a variety of ways, carrying the ideas and practices that emerged from Bradshaw's research forward into contemporary ecological genetics. This analysis provides another view onto the transformation of genecology into ecological genetics, and raises new questions for further research.

This dissertation moves ecological genetics out from the cloisters of Oxford, and into the agricultural research centers of rural Britain. The story of Bradshaw's investigative pathway contributes to our understanding of the historical foundations of ecological genetics and evolutionary population ecology by documenting the changing concepts, aims, and practices of British genecology in the 20th century, through the lens of one of its most prominent practitioners. The entanglement of genecology and British agricultural development raises new questions about the broader historical relationship between evolutionary genetics and plant breeding in the 20th century, and thus contributes to a growing literature on the multifarious linkages between agriculture and the life sciences (Palladino 1996, Kleinman 1999, Kingsland 2008, Harwood 2006, Kimmelman 2006, Bonneuil 2006, Wieland 2006, Matchett 2006, Charnley 2011). Most importantly, this dissertation draws attention to the complexity and plurality of evolutionary theory in the 20th century, the impact of specific research traditions on the foundations of contemporary evolutionary science, and the changing ways in which ecologists and evolutionary biologists conceptualize and investigate variation in the natural world.

Notes on method

This dissertation focuses on the constellation of assumptions, methods, theories, concepts, and imaginations that buttressed and composed the conceptual transformation surrounding the temporal and spatial scale of adaptive evolution in the middle of the 20th century. Science-studies scholars have articulated a variety of operational categories for dealing with those components of scientific research. Those include the thought-styles and thought-collectives of Ludwik Fleck (1935), the paradigms of Thomas Kuhn (1970), the research programmes of Imre Lakatos (1980), and the research traditions of Larry Laudan (1977), among others. What this dissertation draws from each of those accounts is the notion that there are certain contingent regulative aspects of scientific training and discourse that help define what concepts are relevant for the production of knowledge, and give those concepts meaning.

While it is often convenient to use the concepts of "discipline" and "field" to gesture toward the scales on which those processes occur, those concepts are difficult to apply to ecology and evolutionary biology. The fields that draw on or contribute to evolutionary theory are incredibly diverse, often with fluid boundaries. This is especially true in the middle of the 20th century. As Betty Smocovitis (1988) has shown, the very notion of an "evolutionary biology" was a novelty of the Modern Evolutionary Synthesis. Sharon Kingsland (2008) and Joel Hagen (1992) have shown how ecology was continually being reimagined throughout the 20th century, and that these re-imaginations varied across regions, institutions, and lines of intellectual descent. For example, Jane Maienschein (1988) and Sharon Kingsland (1991) have both described specific investigative styles in biology tied to the University Chicago. While the inferences made in this dissertation do not depend on any one particular schematization of such "styles" or "schools," they are linked to the idea

that the particular elements of a research program can be strongly determined by historical factors specific to a locale or community, and that those factors do not map cleanly onto traditional delimitations of scientific fields or disciplines.

Consequently, I have grounded my research in a specific research program exemplifying the conceptual shift that I wish to interrogate, and worked outward to the relevant institutional, disciplinary, and social contexts in which that transformation took place. In so doing, I have drawn on the "investigative pathway" approach of Frederic Holmes. According to Holmes, scientific discovery and change should be understood as a continuous exchange between individual researchers and the natural world, situated within broader investigative traditions. Since the events relevant to this project took place on the scale of months and years rather than days and weeks, I have not taken such an extremely fine-grained approach as Holmes himself has done. Rather, I have used Holmes' approach as a heuristic, and use the questions, methods, concepts, theories, models, and data operative in a particular research program as a lens through which to view not only individual scientists in their engagement with the natural world, but also the institutional, disciplinary, and social factors that contributed to the explanatory frameworks in which that engagement took place.

I have drawn heavily on the Anthony David Bradshaw papers at the University of Liverpool Sydney Jones Library (references beginning with "D1041"), and various archives at the National Library Scotland ("GB449"), the National Library of Wales ("NLW"), and Bangor University ("BU"). In analyzing those archives I focused primarily on field and laboratory notebooks, including notes on experimental design, grant proposals, original data, and drafts of (sometimes unpublished) manuscripts. Correspondence among scientists also helped to illuminate the development of particular research projects, as well as their aims and expectations. Using those archival materials in conjunction with the published primary

research literature generated by Bradshaw and his colleagues provides a far more complete picture of their research activities than would either source in isolation. In some cases I was able to reconstruct both sides of a series of correspondence using material from multiple archives. In addition to archival research, I have also interviewed numerous scientists in the United States, Canada, England, Scotland, Wales, and Switzerland. Named references to those interviews are included throughout the dissertation.

CHAPTER 1: INITIATION

In order to understand the significance of Bradshaw's change of mind about the speed and locality of adaptive evolution, it is important to understand some of the salient factors and influences at the commencement of his investigations. Those factors include the direct and indirect influence of senior members of the scientific establishment, as well as the biological and material factors that converged in Bradshaw's research. In this chapter, I describe some aspects of Bradshaw's entry into the community of plant ecologists in Britain, and his initiation into the theory and practice of plant genecology.

In section 1.1, I describe Bradshaw's training at The University of Cambridge, paying particular attention to the influence of his mentors at that institution: Harry Godwin, Alex Watt, and W. H. Thorpe. Although the aims and methods of Bradshaw's own research diverged significantly from those of his mentors, those scientists did impart certain concepts and attitudes that played consequential roles in shaping Bradshaw's investigative pathway and, ultimately, his ideas about the nature of adaptive evolution. From Godwin, Bradshaw acquired a strongly operational view of ecological concepts, and skepticism toward over-classification. From Watt, Bradshaw came to recognize the significance of microscale environmental variation for ecological processes. Thorpe mentored Bradshaw on a wide variety of subjects, including evolutionary theory, and may have helped to pique Bradshaw's interest in ecological causes of speciation. By the end of section 1.1, Bradshaw is considering his options for graduate research, and reaches out to James W. Gregor at the Scottish Plant Breeding Station.

In section 1.2, I jump back several decades to consider the theoretical and methodological developments in genecological research that occurred at the Scottish Plant Breeding Station between the mid-1920s and the end of the 1940s. This section tells the

story of the "Gregorian" style of genecology: how Gregor interpreted the Scandinavian

botanist Göte Turesson's provocative account of heritable variation in plant populations, its

relationship to agricultural development in Britain, and the ways in which Gregor's

interpretation changed. Those changes were crucial for determining the content and

direction of Bradshaw's early graduate research, and set the stage for his change of mind

about the speed and scale of adaptive evolution.

In section 1.3, I describe Bradshaw's first year and a half as a Ph.D. student at the

Welsh Plant Breeding Station in Aberystwyth, Wales. Bradshaw undertook an ambitious

project on the genecology of agriculturally important herbage grasses that was shaped heavily

by Gregor. Bradshaw's choices of focal organism and sampling strategy were important

factors that enabled his work on microgeographic differentation in the 1950s and '60s.

1.1. Cambridge

Tony Bradshaw entered Jesus College, Cambridge, in the autumn of 1944,[2] near the end of

the Second World War. Bradshaw's childhood bore some characteristic features of war-time

life. He took charge of the family's "victory garden"—spinach in the front garden, tomatoes

in the back—taking pains to remediate the "horrible London clay" at their Hampstead home

with compost and ash. His secondary school, St. Paul's at Hammersmith in London, had

been evacuated westward to Crowthorne in Birkshire County to avoid the air raids.

Returning to Hampstead on school holidays meant frequently "snuggling down" in the air

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[2] Contrary to Fitter (2010). Bradshaw was still participating in activities at St. Paul's School in
Hammersmith, his secondary school, in the summer of 1944. He had expected to finish
the Natural Sciences Tripos in spring of 1947.

raid shelter in the dining room: first a homemade brick structure, and later a Morrison "mouse trap" shelter made of steel plates and mesh (D1041/13/2/9).

Bradshaw's path into the Natural Sciences Tripos at Cambridge was paved in part by the mentorship of his high-school biology teachers at St. Paul's, Tony Barnett and Barnett's successor Sidney Pask. Pask was known both for his severe personality in the classroom, and for his contagious passion for biology.[3] Pask would often stay late after school, encouraging his students to pursue research projects in their free time.[4] Bradshaw took him up on the challenge, testing the effects of different fertilizers and manures on the yield of ryegrass, seeds of which Bradshaw had obtained from the Welsh Plant Breeding Station in Aberystwyth (D1041/13/2/9). Bradshaw took an interest in learning to identify the various

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[3] Oliver Sacks, who started at St. Paul's in 1946, describes Pask as "...a splendid teacher. He was also narrow-minded, bigoted, cursed with a hideous stutter (which we would imitate endlessly), and by no means exceptionally intelligent. By dissuasion, irony, ridicule, or force, he would turn us away from all other activities—from sport and sex, from religion and families, and from all our other subjects at school. He demanded that we be as single-minded as himself. The majority of his pupils found him an impossibly demanding and exacting taskmaster. They would do all they could to escape from this pedant's petty tyranny, as they regarded it. [...] Yet some of us, each year, responded to Pask's challenge. In return he gave us all of himself—all his time, all his dedication, for biology. We would stay late in the evening with him in the Natural History Museum... We would sacrifice every weekend to plant-collecting expeditions" (Sacks 2001).
ICL Professor of Science and Society Robert Winston remembers Pask more sympathetically: "Sid was crucial in my development. He was witty, open-minded, inquiring and enthusiastic, and he was able to see what was sensible and what was not. He was able to focus on the things that were likely to stimulate us." Winston, Robert. 2009. "My Best Teacher." TES Newspaper.

[4] According to television director Jonathan Miller, "Lunchtimes were for carrying out more dissections, and as far as Mr. Pask was concerned, that applied to holidays too. At weekends in the winter he took us to the Natural History Museum where we drew diagrams of vertebrates and considered evolution. In the summer we went on excursions by train into the suburbs to collect plants, press them and learn to classify them" (Miller 2007).

grass species in the fields around Crowthorne, and upon entering Cambridge he anticipated a career in agricultural research (D1041/13/2/9).

Bradshaw was not especially engrossed with his academic pursuits at first,[5] but by the spring of his second year at Cambridge he was increasingly drawn to ecological research. He was especially "bewitched" by the experimental ecology of Harry Godwin (1901–1985), who would become one of Bradshaw's foremost undergraduate mentors (D1041/13/2/9).

1.1.1. Harry Godwin

Bradshaw's fascination with Godwin revolved primarily around his experimental approach to community ecology. Godwin's ecological interests were heavily influenced by his own undergraduate mentor, Arthur G. Tansley. As a student at Clare College in the 1910s,

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[5] As early as his secondary-school days at St. Paul's, Bradshaw had a passion for the performing arts. His name could be found on programs for The Devil's Disciple, performed in the summer of 1944 at St. Paul's (on occasion of a visit by the U.S. Ambassador to the U.K., John G. Winant; July 7, 1944) and as a dancer in Dido and Aeneas at Jesus College (D1041/13/2). At Cambridge, Bradshaw founded the College Chorus, participated in the Jesus College Musical Society, and organized a variety of musical events. (D1041/13/2–3) Bradshaw was also an avid boater, a passion no doubt catalyzed by the assortment of boats at the family cottage at Waxham in Norfolk (D1041/13/2/9). At Jesus College, Bradshaw traded in the reed-bending 'coot' (A small pram dinghy) of his summertime youth for the elegant rowing shell. At the Lent Races of 1945 Bradshaw rowed 7-seat in the College's third eight, and by the May Races that year he advanced to the "fastest second boat on the river," placing ninth among all eights in the University. "7-seat" is the rower directly behind the "stroke," or aft-most rower in a traditional eight-person rowing shell. Those two rowers – known as the "stern pair" – work closely with the coxswain (a ninth person, seated in the very stern of the shell, responsible for steering and directing the boat) in providing leadership to the rest of the crew by setting the rhythm and pace of rowing. Boats within a rowing program (such as a college Boating Club) will be ranked according to speed, with the fastest rowers in the "first" boat (D1041/13/2). Having joined the Air Scouts and serving as Assistant Scout Master at St. Paul's, Bradshaw was an active participant in the The University of Cambridge Scout Group. Bradshaw served as Junior Treasurer, and Representative for Jesus College, in 1948 (D1041/13/2).

Godwin frequently accompanied Tansley to an area of marshland near the village of Wicken, around ten miles northeast of Cambridge, which would become the focus of Godwin's graduate research (West 1988). Both Tansley and Godwin were interested in succession, the process by which an ecological community successively gives way to another. One of the predominant patterns of succession in East Anglia involves the transition from fresh water lakes and ponds to shallow marshland through the accumulation of peat, and eventually to deciduous woodland. Tansley and Godwin saw Wicken Fen as a mid-point in such a "hydrosere" succession, and therefore an opportunity to study the mechanisms of succession in action (Godwin 1929, 1931).

Compared to Tansley, however, Godwin's research style had a far more quantitative and experimental tendency. Compelled by American ecologist Frederic Clements' calls for an experimentally sophisticated ecology, Godwin sought to cultivate an experimental approach in his own work by pursuing his Ph.D. under the supervision of plant physiologist F. F. Blackman, instead of Tansley (West 1988). In 1923 Godwin commenced a series of studies at Wicken Fen, which involved manipulating factors like water level and defoliation, and generating quantitative data about the distribution and abundance of plant species in the experimental plots (Godwin 1929, 1931, 1936, Godwin & Bharucha 1932). The site of those studies is now known as the "Godwin Plots," where some of Godwin's original cutting experiments continue to be maintained. Godwin's work at Wicken Fen suggested that cutting could have a profound effect on the trajectory of succession in the Fen, which led him to view the Fen not as an example of unaltered "natural" succession, but rather a reflection of historical land management practices (West 1988). During Bradshaw's years at Cambridge, Godwin established a Subdepartment of Quaternary Research at Cambridge,

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which integrated geological, anthropological, and botanical approaches to investigate the history of vegetational change in Britain (Godwin 1929).

Tansley and Godwin shared a suspicion of abstract taxonomies in science, an intellectual style that Bradshaw also exhibited. Tansley and Godwin's ideas about succession and ecological communities fell somewhere around the mid-point of the continuum between those of Clements and American botanist Henry Gleason. Clements saw communities as super-individual entities, even super-organisms, and succession as a highly deterministic ontogenetic process similar to the development of individual organisms. As a consequence of that idea, Clements attempted to identify and categorize distinct types and stages of succession. Gleason, in contrast, rejected entirely the idea that communities or associations were anything but chance co-incidences of species with similar physiological tolerances, thought that the project of classifying those communities and their successional stages yielded no substantive scientific insight (Gleason 1926, 1927). Tansley adopted a distinctly operational perspective. In a critical response (titled "The use and abuse of vegetational concepts and terms") to a series of pro-Clementsian papers written by South African plant ecologist John Phillips in the mid-1930s, Tansley limited his endorsement of the concepts of succession and the "organismal" community. Tansley saw value in those concepts only to the extent that they could direct attention to the complex interactions of abiotic and biotic factors, and generate new insights about the mechanisms of vegetational change (Tansley 1935, Willis 1997). Godwin also distanced himself from Frederic Clements' categorization of deterministic successional stages, and instead saw successional change as a contingent product of the physiological responses of individual plants to environmental factors.

In the spring of 1946, Bradshaw tried his hand at Godwin's methods at Hickling Broad, near the vacation cottage at Waxham where the Bradshaws spent their summers at

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play on the water. He must have have thrown himself enthusiastically into the work. At the Cambridge Natural History Society's annual research symposium (known as the "Conversazione") in May, Bradshaw gave not one but two presentations: one on "Aspects of the hydrobiology of Hickling Broad" and another on "Fen succession" (D1041/13/2).

Although Bradshaw did not pursue community ecology further, he retained Godwin and Tansley's operational perspective on ecological concepts, and especially Godwin's skepticism about over-taxonomizing ecological phenomena. Just as Godwin and Tansley had devoted a substantial portion of their 1929 volume, The Vegetation of Wicken Fen, to a reflection on the role of "some modern ecological conceptions" in guiding and constraining ecological research, so too did Bradshaw's essays at the start of his graduate career dwell on the cognitive role and epistemic status of the "community" concept. Indeed, Bradshaw opened one essay, written in the autumn of 1948, with the assertion that a major flaw of mainstream ecological research was a focus on subjective classifications that "depended on some preconceived ideas as to the nature of the plant community," shaped by the specific features of the landscapes in which ecologists have found themselves (D1041/1/11/87, p. 1). In discussing the Clementsian conception of the community as organism, Bradshaw wrote, "I hope to show that this is an over-simplified picture. It suggests that vegetation resolves itself into discrete stable units. If one is faced with the problem of classifying vegetation then ones wishes might well be father of this thought!" (D1041/1/11/87, p. 2).

1.1.2. Alex Watt

That summer, during the "Long Vac" term of 1946, Bradshaw had the opportunity to take part in field trips led by Godwin and other members of the natural sciences faculty. It was a radical change from the stale coursework of the regular term, and Bradshaw was excited to

participate in Clifford Evans' experimental physiology labs, "growing and handling whole, live, plants" (D1041/13/2/9). It was also an opportunity for Bradshaw to interact with Scottish botanist Alexander "Sandy" Watt (1892–1985), who would also become a significant mentor.

Bradshaw encountered Watt just as Watt was articulating what would become a highly influential approach to investigating plant communities, now known as "patch dynamics." Like Tansley and Godwin, Watt attempted to find a middle road between the determinism of Clementsian succession and Gleason's "individualistic conception" of ecology. In contrast to Clements' directional model of succession, Watt saw vegetational change as cyclic. Most importantly, Watt emphasized the role of spatial heterogeneity in shaping patterns of vegetational change. In his presidential address to the British Ecological Society in January, 1947, Watt argued that plant communities should be understood as "working mechanisms," each composed of a mosaic of heterogeneous patches characterized by different environmental factors and particular aggregations of individual organisms (Watt 1947). According to Watt, the dynamics of an ecosystem could only be understood with reference to the distribution and dynamics of those patches, each of which might be as small as a few centimeters (Watt 1947, Greig-Smith 1986).

The idea that environmental heterogeneity on very small spatial scales could have a significant impact on ecological processes was compelling for Bradshaw, although he had not yet considered its implications in an evolutionary context. Bradshaw wrote in 1948:

> [Watt] noticed that the mature community was not by any means even, but
> consisted of innumerable patches … each probably not more than 2 inches
> across. […] All this suggests rather a dynamic view of the community. There
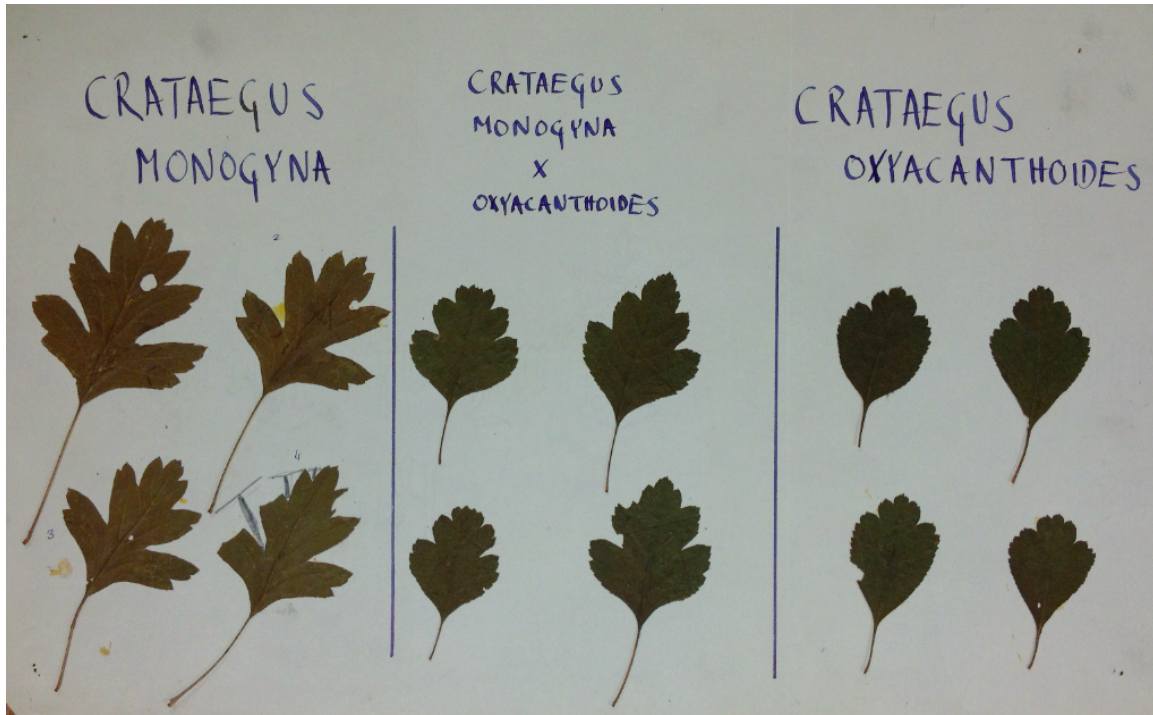
Figure 1.1.1. Pressed hawthorn leaves from undergraduate project with Robin Cuany. Second from the left in the bottom row shows degree of leaf indentation, although the lobe tips are broken off. Courtesy of the University of Liverpool Sydney Jones Library Special Collections & Archives.

> is little in these communities which resembles an organism; there is no static
>
> organisation, but a structure that is permanently changing with time.
>
> (D1041/1/11/87, p. 3)

Bradshaw emphasized the importance of environmental heterogeneity on small spatial scales for understanding the composition of local assemblages, asserting that the complex overlay of climate, soil factors, local topography, and interspecific interactions conspired to produce "discontinuous local environments."

1.1.3. Crataegus

The Long Vac term of 1946 was also a chance for more ambitious attempts at research, and it was in that context that Bradshaw developed an interest in the relationship between

ecology and genetics. That summer Bradshaw and his close friend, Robin L. Cuany undertook a study of hawthorns (*Crataegus*) in southeastern Britain as an independent research project. The genus *Crataegus* contains a variety of shrubs and trees in northern temperate climates. The common hawthorn, *C. monogyna*,is a ubiquitous feature of the British landscape. At the time, *Crataegus* was especially vexing from the standpoint of taxonomy due to the potential for widespread hybridization among the more than 1,100 described species in the genus (Camp 1942). Bradshaw and Cuany wondered whether anthropogenic disturbance of woodlands had an effect on the hybridization between two hawthorn species: the midland hawthorn, *C. oxyacanthoides* (now *C. laevigata*), which prefers dense woodland, and *C. monogyna,* which prefers more open areas. They hypothesized that fresh clearings within woodlands provided opportunities for *C. monogyna* to become established in close proximity to *C. oxyacanthoides*, leading to greater opportunities for hybridization (Bradshaw 1953).

Bradshaw and Cuany started their fieldwork on an ambitious day at the end of July, 1946, collecting leaves along transects in Fordham village and the nearby Chippenham fen, northeast of Cambridge, before traveling to the Park Wood in Ruislip, northwest of London. Using the degree of leaf indentation[6] as a diagnostic character, they compared the distribution of morphologies in each population, assuming that hybrids would exhibit a form intermediate to the two parental species. Bradshaw and Cuany took the project very seriously, keeping meticulous notes and revisiting sites to improve sample sizes as needed. Throughout August they made trips to Hardwick Wood, Buff Wood, and Barton Close, and

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[6] Measured from the sinus between the first two lobes to the line connecting the lobe-tips (D1041/2/43).

afar to Clandon and Croydon, south of London. The more that they worked, the more exciting the work seemed to them: the hawthorns growing in "hybrid" habitats did indeed appear to show an intermediate morphology to the two parent species. When in early September they veered east to Maidstone and Rainham, in Kent, they found some of the most distinctly "pure" populations of the two Hawthorn species, a stark contrast to the more extensively hybridized populations that they had found elsewhere in southern Britain (D1041/3/5).

That winter, however, the growing momentum behind Bradshaw's scientific training was deflected by an unexpected change in the environment, with both disastrous and fortuitous consequences. The winter of 1946 and 1947 was infamously bitter. Coal supplies across Britain were perilously low in the wake of the war, and as the temperature dropped precipitously in late January power plants across the country were unable to keep up with demand (Robertson 1987). As the cold set in, Bradshaw was confined to his bed with a severe case of pneumonia. February saw the coldest temperature on record for many parts of Britain,[7] followed by heavy snowdrifts in early March. The dormitory at Jesus College was so cold that, on three occasions, Bradshaw had to break ice from the top of the ewer beside his bed so that he could wash (D1041/13/2/9).

As the snowmelt floodwaters subsided in the spring of 1947, and Bradshaw ventured from his sickbed, his thoughts turned to the imminent final exams that were to mark the end of his undergraduate studies. Bradshaw invited Cuany and their friends Peter and Ral to his

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[7] A mean maximum temperature of 0.5 C was recorded at the Kew Observatory for the month of February, and a low of -21 C was reported on February 25th at Woburn, Bedfordshire, about 40 miles west-southwest of Cambridge. http://www.metoffice.gov.uk [Accessed 11 Feb, 2013]

family's cottage at Waxham, hoping to gain some mental clarity in advance of the exams (D1041/2/4/2). Bradshaw showed his friends around Hickling Broad and, at the prodding of some of the "more serious members of the party," the group carried out a survey at East Ruston Common, identifying species at 22 stations along a 300-meter transect. Bradshaw later recalled the trip fondly: "The way different species had their own particular places in the transect was fascinating. It taught me much about ecology" (D1041/13/2/9).
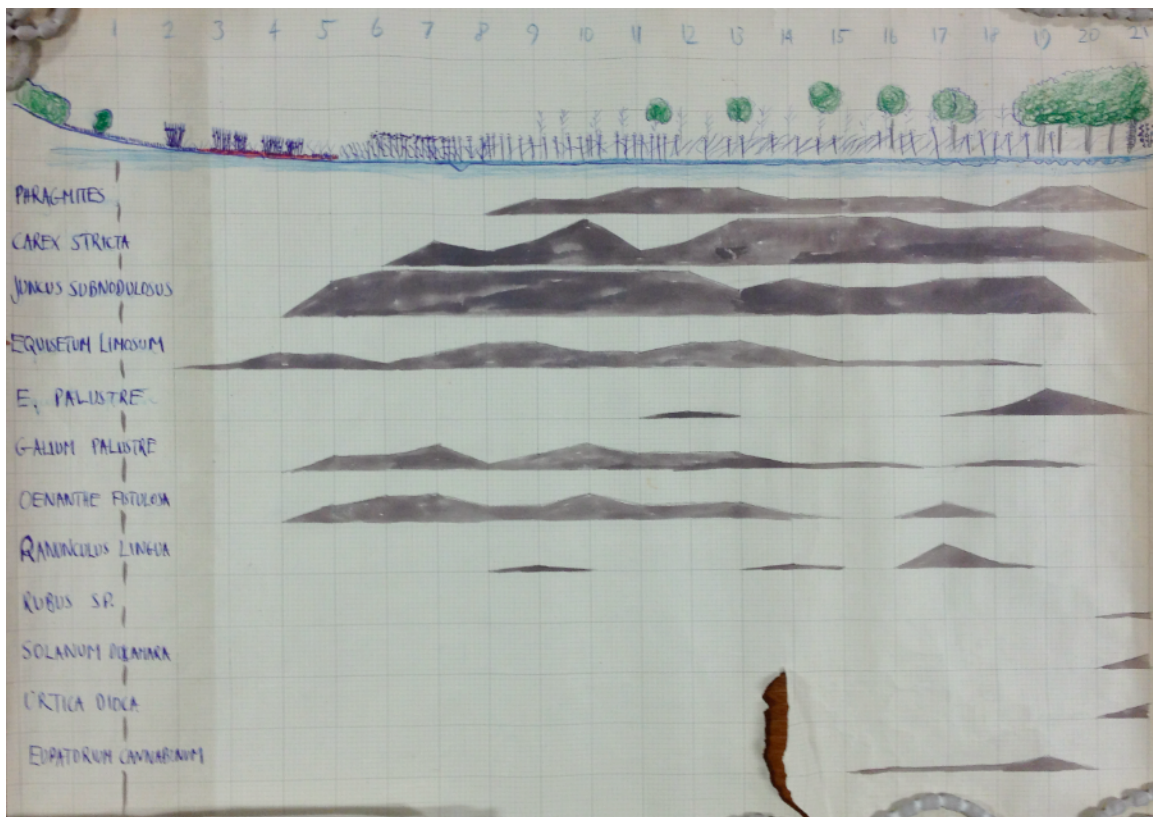
Figure 1.1.2. Illustration of transect at East Ruston Fen, 1947. Courtesy of the University of Liverpool Sydney Jones Library Special Collections & Archives.

Yet when it came time for Bradshaw to sit his final exams, the damage done by his winter illness was irreparable. He had simply missed too much coursework to achieve a passing grade, and was forced to retake a large portion of his third-year courses. Although

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the immediate effect was undoubtedly one of disappointment—long had Bradshaw harbored

feelings of scholastic inferiority to his older siblings (D1041/13/2/9)—the delay ultimately

proved a valuable opportunity. Repeating his third year allowed Bradshaw to participate in

the long-vac excursions for a second time, consolidating his relationship with his mentors

Godwin and Watt.

The extra year was also an opportunity to build on the hawthorn project that he had

started with Cuany the previous summer. This provided an *entré* into a broader community

of ecologists. Godwin and Watt encouraged Bradshaw to present the results of the

Hawthorn project to the British Ecological Society (of which Godwin was then Secretary,

and Watt was then President) at their annual meeting, in January of 1948. In advance of the

meeting, Bradshaw's friend Marianne (a student at Newnham College) teased him about his

impending presentation, writing on the back of a carefully detailed sketch of a hawthorn leaf:

> I think your arithmetic is bound to be faulty. Your ecology, however, is not!
>
> Hence, what this is really for, is to wish you well on 9-1-48. I shall attend the
>
> great occasion with bated breath. [rib. This is "7/8 serious".] Love, Marianne.
>
> (D1041/13/2/7)

Bradshaw needed the well-wishes a bit sooner than he had expected. On the morning of the

first day of the meeting, Bradshaw "nearly miffed it:" "[I] got to Paddington Station to go to

[Bristol],[8] [and] met Harry Godwin who in a very friendly greeting said 'have you got your

slides?' No answer from me—I just turned and fled back to Hampstead." (D1041/13/2/9)

Friday went more smoothly, however, and Bradshaw's presentation sparked an "active

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[8] Bradshaw later remembered the site of the meeting as Oxford, but the minutes (published
in *Journal of Ecology*, 36: 193-197) place the meeting at the Departments of Botany and
Zoology, Bristol University.

discussion" among both junior and senior ecologists, including Geoffrey Blackman, William

Harold Pearsall, Arthur Roy Clapham, Charles S. Elton, and Herbert G. Baker.[9] As

Bradshaw later described the event, "in one fell swoop I was fledged as a botanist with a very

rewarding problem which even excited other people" (D1041/13/2/9).[10] By the time that

Bradshaw sat his final exams for the second time, he was excited about continuing on into a

research career.

1.1.4. A Change of Direction

In his final year at Cambridge, Bradshaw preferred the idea of staying on there to do

ecological research under Godwin. But Godwin insisted that Bradshaw seek out "new

ideas." Bradshaw also consulted Australian botanist and pedologist Robert Langdon Crocker

(1914-1963), who had arrived at Cambridge the year before on a Rockefeller fellowship.

Crocker and Gregor agreed that Bradshaw should contact James W. Gregor to explore the

possibility of working at the Scottish Society for Plant Breeding in Corstorphine, near

Edinburgh.

Although Bradshaw was excited about research, and entertained the idea of obtaining

a Ph.D., he was not particularly excited about an academic career. In a letter to Gregor that

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[9] Discussants included: Robin L. Cuany, Bradshaw's partner on the Hawthorn project;
Geoffrey E. Blackman, Sibthorpian Professor of Rural Economy, Oxford; William Harold
Pearsall, Quain Professor of Botany, University College London; Arthur Roy Clapham,
Chair of Botany, University of Sheffield; Charles S. Elton, Bureau of Animal Population,
Oxford; Herbert G. Baker, Lecturer, University of Leeds; Edmund. F. Warburg, University
Demonstrator in Botany & Curator of the Druce Herbarium, Botany School, Oxford;
Victor S. Summerhayes, Herbarium curator, Kew; Alfred J. Wilmott, British and European
Herbarium, British Museum of Natural History; Alex S. Watt; Harry Godwin.

[10] Bradshaw would continue to write about Crataegus throughout the 1950s, presenting his
work the Botanical Society of the British Isles, fielding queries from amateur naturalists,
and contributing descriptions for the *Biological Flora of the British Isles.*

April, Bradshaw admitted that, "I have always been most interested in the practical side of anything I have had to do, so I have rather fought shy of any work that would be too academic" (GD449/5/10). Bradshaw's work on hawthorns had awakened his interest in the relationship between ecology and genetics. The chair of the Botany Department at Cambridge, Professor F. T. Brooks, suggested that (in light of his interest in applied research) Bradshaw apply for a Studentship from the Agricultural Research Council to carry out "genetical-ecological" work on grasses. "Grasses were suggested," Bradshaw told Gregor, "because of the awakening interest that there is in them and the likelihood of there being suitable posts vacant later on" (GD449/5/10). Indeed, as I describe in section 1.2.3, the importance of pastureland grasses for the British economy during this period cannot be overstated.

Gregor replied to Bradshaw a few days later, and tried to reassure him about the value of a Ph.D. for a research career. "Despite the many unkind things that have been said about its merit the Ph.D. remains a valuable qualification to have when applying for a research post. I favour taking the Ph.D. before looking for a job, that is while one is still free to choose the subject, and still unhampered by routine duties. This means acquiring a scholarship and Professor Brooks' suggestion of an A. R. C. [Studentship] is a most excellent one" (GD449/5/8). Although Gregor strongly preferred to meet Bradshaw prior to making decisions about whether he would pursue his Ph.D. research at Corstorphine, he noted the impending deadline for an application to the A. R. C. and thus agreed to the arrangement.

Over the next several weeks, Gregor and Bradshaw continued to discuss ideas for a proposal to the A.R.C. Gregor intimated to Bradshaw that the younger ecologist's interest in "genetical-ecological" research "offers far more scope for original work" than "purely ecological" research (GD449/5/8). Gregor framed what he took to be the more promising

direction of investigation in terms of the genetic variation underlying the "ecological tolerance" of plant species.

> There is already a mass of data - not always very reliable data it is true - from which it is possible to say that this or that taxonomic species prefers this or that kind of habitat; in other words, that such and such a species possesses a certain ecological tolerance. That is all right so far as it goes, but what we really need to know is the genetic pattern of this tolerance: is it ecotypic, or ecospecific, or a combination of both? In the first place we require to examine the composition of the taxonomic species, the unit used by the ecologist, and determine whether or not it is truly divided into more or less independent genetic units - ecospecies, and then determine the ecological distribution of variation within these groups… (GD449/5/8).

Many of the terms and phrases that Gregor used in his letters—ecotypes, ecospecies—may have been new to Bradshaw. Nevertheless, Gregor's mandate would form the basis of Bradshaw's research program.

In order to understand the substance of Gregor's influence on Bradshaw, we must consider the development of Gregor's own research and ideas. In the mid-1920s, Gregor began to work in the field of genecology, what was then a new and provocative direction for plant ecologists that had recently been articulated by botanist Göte Turesson in Scandinavia. In the following section I describe Gregor's initiation into the field of genecology, the development of his research at the Scottish Plant Breeding Station, and his changing interpretations of the concepts, aims, and

methods for genecology. Gregor's approach to genecology formed the launchpad for

Bradshaw's research, and shaped its content and direction in substantial ways.

1.2. Gregorian genecology

James Wyllie Gregor (14 January, 1900–30 September, 1980) was born on Innerwick Farm

near the village of Innerwick, some thirty miles due east of Edinburgh, at the very eastern tip

of the East Lothian district. Historian Arthur Granville Bradley recalled his visit to the area

in the 1870s as an exemplar of British agriculture:

> The rolling plain of East Lothian begins at Pease Pass and Cocksburnpath in
>
> a narrow strip between the sea and the hills, and gradually expands in a
>
> fanlike shape as you travel westward in the direction of Edinburgh. This is a
>
> country with a character entirely its own … unlike any other in Scotland, and
>
> still more unlike … any in England. It might be likened to a vast garden lying
>
> between a rocky, broken coastline and a wild waste of moor. … It is a garden
>
> of twenty- or thirty-acre fields geometrically laid out and divided by stone
>
> walls or thorn fences, upon either side of which no foot of space is given to
>
> the unprofitable or the picturesque in nature. Turnips, barley, seeds, oats,
>
> potatoes, wheat, as the old rhymical *memoria technica* of the East Lothian six-
>
> course shift had it, may be roughly taken as indicating the composition of the
>
> rich-coloured patchwork that lays along the levels and climbs the low hills.
>
> … At intervals stand the great farm steadings, bearing to one another a
>
> certain family likeness not common in the south, and giving an appearance of
>
> formality which is strengthened by the tall unlovely chimneys of the
>
> stationary engines, though somewhat ameliorated on the other hand by the

warm red sandstone walls and red-tiled roofs of the out-buildings and

cottages. (Bradley 1912, pp. 265–267)

The Innerwick Farm was part of a large estate sold off by the Gorings, a wealthy Scotish

political family, in the 1620s (Baggs and Warne 1997). The Farm sits in the fertile coastal

plain, nestled between the North Sea coast, about a mile and half to the east as the crow

flies, and the rolling uplands of Lammermuir ("Lamb's Moor") Hills to the southwest. At the

time that Gregor was born, his parents leased a part of the farm, perhaps one or two

hundred acres, from its owner F. J. Neale. The Gregor's would likely have grown some

combination of wheat, swede (rutabaga), and oats.

Between the ages of eight and thirteen Gregor attended a Catholic school[11] in

Melrose before attending The Edinburgh Academy, a small private school, between 1914

and 1917 (Royal Society of Edinburgh). Gregor served in the Royal Flying Corps from 1917

to 1919 (Foister, 1978). After his stint in the military, Gregor attended Edinburgh and East

of Scotland College of Agriculture, where he was greatly influenced by Scottish plant

ecologist William G. Smith (Anon 1966). Smith was a founding member and the inaugural

secretary of the Central Committee for the Study and Survey of British Vegetation, a pre-

cursor of the British Ecological Society (Salisbury, 1964; Gimingham, 2003).

After receiving his diploma in 1924, Gregor was hired by the Scottish Society for

Research in Plant Breeding to work at their research station at Craig's House in

Corstorphine, on the west side of Edinburgh. A year later, in 1925, he was promoted to

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[11] St. Mary's Preparatory School

Chief Assistant, and put in charge of breeding herbage[12] plants and potatoes, as well as overseeing fieldwork at the station (GD449/7/306). In 1930 his responsibilities narrowed to the herbage program alone, allowing Gregor to devote more time to genecological research. Gregor remained at the SPBS throughout his career, where he served as director from 1950 until his retirement in 1965.

The Scottish Plant Breeding Station (SPBS) was established just a few years prior to Gregor's arrival, in response to regional tensions over seed production and testing that arose during World War I (Paladino 2003). Dissatisfaction among British farmers over the quality of agricultural seed imported from Europe during WWI prompted the Food Production Department to establish an Official Seed Testing Station in Cambridge, which was subsequently incorporated into the National Institute of Agricultural Botany (NIAB). Although the station in Cambridge was billed by the government as a service center for all of Britain, Scottish farmers felt that it was insufficient to meet their needs: tests performed in the dry, continental climate and silty sandy soils of Cambridgeshire yielded little, if any, information about how seeds would perform in the wetter, loamier conditions of Scotland.

The Scottish Society for Research in Plant Breeding, a consortium of Scottish land owners and seed companies, thus established the SPBS in 1921 as a commercial membership-based venture to produce high-quality seeds specially suited to the needs of Scottish farmers, which would be multiplied and distributed by member seed companies. Plans for the Station quickly drew interest from the Development Commission and the Department of Agriculture for Scotland, who provided a large grant to launch the project.

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[12] "Herbage" refers to herbaceous vegetation (usually grasses) used for stock grazing.

Ultimately a deal was struck in which the Cambridge Station would focus on wheat and barley, while the SPBS would focus on potatoes and oats.

James Montagu Frank Drummond (1881–1965), the first director of the SPBS, shaped the intellectual culture of the Station, as well as Gregor's own views on the relationship between plant evolution and agricultural development. Drummond was a taxonomist with interests in genetics and evolutionary theory. Drummond attended Kings College, London, before holding the Frank Smart Research Studentship at Cambridge from 1904 to 1906. Prior to working at the SPBS, Drummond lectured in Botany at both Newcastle-upon-Tyne (1906–1909) and Glasgow (1909–1921). As Paladino (2003) notes, Drummond's taxonomic background made him particularly well suited for making sense of the "bewildering number of varieties of potatoes found on the market" (Paladino 2003, p. 49). Drummond saw the clarification of variation and its genetic basis as a precondition for a successful breeding program.

In October of 1926, Drummond made a presidential address to the Botanical Society of Edinburgh. Drummond's paper, titled "Some reflections on the nature of species," provides a window on how Turesson's genecology was interpreted at the SPBS in the 1920s. In the following section, I describe the intellectual context and core tenets of Turesson's genecological theory from the perspective of Drummond. That is, I have selected and arranged the material discussed here such that it mirrors the main contours of Drummond's 1926 discussion of species concepts. This is helpful for understanding the ideas to which Gregor was exposed in his first few years at the SPBS, and provides a starting-point for understanding the evolution of Gregor's ideas about ecotypes and genetic differentiation of populations over the subsequent several decades.

1.2.1. Species, Ecotypes, and the Problem of Variation

Drummond's task of making sense of the potato market mirrored a more fundamental problem in the life sciences, the problem of variation. That variation in the characteristics of plants and animals is not a continuous smear, but rather a lumpy hodgepodge of more-or-less distinguishable and separable forms and varieties has occupied the minds of observers of the natural world for several millennia. Aristotle's *Historia Animalium* is widely considered the first concerted attempt to systematize that lumpiness. Aristotle recognized that our ability to recognize abstract forms—to differentiate plants from animals, or birds from insects—in the fog of organismal variation is crucial for being able to reason about the natural world, and even to reason about the properties and behaviors of individual organisms. On the other hand, as Aristotle recognized, such differentiations can be made all the way down to the level of individual organisms, as no two individuals are exactly alike. The problem of variation is thus to find the sweet-spot that captures and systematizes the apparent discontinuities of organismal variation without descending into the regress of recording the characteristics of each individual organism that one encounters.

The lower level at which one cuts the living world into distinguishable forms or types is informed partly by one's theory about why those forms or types might exist in the first place. One of the most influential attempts at such a system was the one offered by Swedish botanist Carl von Linné (1707–1778), self-styled as Corolus Linnaeus, in the 18th century. The Linnaean taxonomy consists of a "system of nested classes whose members are individual organisms" (Buck and Hull 1966), organized on the basis of their morphological characteristics. Each of Linnaeus' three kingdoms—the plant, the animal, and the mineral— has several classes. Each of those classes, in turn, has several orders, which can be further

subdivided into several families. The Linnaean hierarchy bottoms out at the rank of species. Species were, for Linnaeus, the fundamental forms or types created by God at the beginning of Earth's history. "Species are all those diverse forms which the Infinite Being produced in the beginning," Linnaeus wrote; "each of these forms has produced, in accordance with the laws of generation, more like unto itself. Hence there are as many species as there are at the present day different forms and structures (Linnaeus, 1750, Aphorism 157; as translated in Drummond, 1926). Distinctions below the species level were certainly possible in the Linnaean system, but were afforded a lower level of significance. A variety within a species was, according to Linnaeus, a subsequent modification of the species due to "an incidental cause such as climate, soil, heat, wind, etc." (Linnaeus 1750, note for Aphorism 158, as translated in Drummond 1926).

As Drummond (1926) notes, Linnaeus' conception of species seems to foreshadow the two criteria of species identity used at the turn of the 20th century: (1) morphological similarity, and (2) faithful reproduction, or "breeding true to type." Although the supernatural interpretation of species was shed by most naturalists of the 19th century, what persisted in taxonomic practice was the hypothesis that coherent species could be distilled from the mess of morphological variation, and that those specific groupings represented some stable type or form, variations on which were relatively incidental or transient.

According to Drummond, during the 19th century the Linnaean conception of biological species came under fire from three directions: the idea that Linnaean species are mutable, the observation that they are frequently divisible into smaller coherent units, and the stipulation that a modern concept of species accord with the concepts of 20th-century genetics.

The idea that biological species were not fixed types, but represented merely a moment along an evolutionary progression, began to gain scientific traction in the early 19th century. Jean-Baptiste Lamarck (1744–1829) was among the foremost transmutationists of that period. Lamarck's evolutionary theory, which he proposed in his 1809 *Philosophie Zoologique*, held that simpler organisms would, through the action of internal forces (e.g., the "subtle fluids"), attain greater and greater levels of complexity, producing a sequence of specific forms. The diversity of biological species, in Lamarck's system, was the product of independent parallel lines of transmutation from unorganized matter to complex multicellular organisms. Another proponent of transmutation, Charles Robert Darwin (1809–1882), postulated that the diversity and discontinuity of variation in organisms was due to a process of divergence and modification. According to Darwin, a group of interbreeding organisms (a species, perhaps) might become fractured and the contrasting environments in which the resulting groups resided would, either through the inheritance of acquired characteristics or by natural selection, take on new forms and modes of life. In the Darwinian view, the Linnaean hierarchy—species grouped into genera, genera into families, and so on—is explained by this very process of divergence and gradual differentiation.

The Darwinian view of transmutation and diversification had both a reifying and an undermining effect on the concept of species. On one hand, the existence of species is important evidence for the Darwinian concept of descent with modification. The fact that the whole of organismal variation is not just a smear of intergradations and continua, but at some level discrete and delimitable, was an important part of Darwin's theory. Darwin wrote, "To sum up, I believe that species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links" (Darwin 1860, p. 177). The reason for such extricability, Darwin goes on to explain, is the

extinction of intermediate varieties. On the other hand, the idea that those groupings reflected selection of individual, heritable variations undermined the status of species as a primary or even special unit of evolution. If individual variations were the primary object of selection, then on what basis should the naturalist cease to make finer and finer discriminations among variants within a species? Darwin wrote that, "In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species" (Darwin 1860; p.486). Species were thus an important interface between the discontinuities produced by millions of years of divergence and descent and the intergradations of individual variation, but without any special reality apart from convenience of reference.

Not only did transmutation challenge the fixity of the Linnaean species, but it also raised questions about the aims of the taxonomic project. Is it the task of taxonomy to simply record and systematize the apparent divisions of organismal variation as it is presently found? Or ought taxonomic categories—if even just the rank of species—correspond to units of evolutionary change?

A second line of attack on the Linnaean species was the idea that many such established species could be further divided into smaller, distinctive, and stable units. This view is usually associated with the work of French botanist Claude Thomas Alexis Jordan (1814–1897) and Dutch botanist Hugo Marie de Vries (1848–1935). Jordan used a combination of morphological analysis and cultivation experiments to identify and delimit sub-specific "petites éspèces" that he believed were immutable—for he rejected Darwinism—and more fundamental than Linnaean species. The Dutch botanist Johannes

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Paulus Lotsy (1867–1931) coined the term "Jordanon" to refer to those species *sensu* Jordan. De Vries, who referred to Jordanons as an "elementary species," adopted a similar view. "The systematic species, as they are accepted nowadays, are as a rule compound groups," De Vries contended, "Sometimes they consist of two or three, or a few, elementary types, but in other cases they comprise 20, or 50, or even hundreds of constant and well-differentiated forms" (De Vries 1905, p. 38). Jordan placed special emphasis on "faithful reproduction"— that the offspring of members of a particular type retained similar characteristics—as a criterion of *petites éspèces* status.

A third and complementary factor undermining the Linnaean conception of species was the rise of genetics around the turn of the 20th century. This involved both the rediscovery of Moravian botanist Gregor Mendel's model of heredity, as well as the articulation of the genotype-phenotype distinction by Danish botanist Wilhelm Johannsen around 1905 (Churchill 1974, Sapp 1983, Roll-Hansen 2009, Peirson 2012c). Mendel's experiments on heredity in peas suggested a particulate view of inheritance: that the heritable characteristics of organisms are to a certain degree divisible and independent of each other (Bowler 1983). Johannsen's work on pure lines in barley suggested that lineages could be isolated, corresponding to a fixed genotype (Peirson 2012c).

If species are units of evolutionary change, what then is the relationship between the sub-specific Jordanon, or elementary species, distilled from the variations of natural populations, and the pure lines or "homozygous races" given by theory and laboratory experiments? For some, including Lotsy, the most logical interpretation was that they were one and the same. Indeed, Lotsy criticized Jordan's criterion of "faithful reproduction" on the grounds that, in light of Mendel, such a test did not give full assurance of genetic purity. "A species consists of the total of individuals of identical constitution unable to form more

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than one kind of gametes," Lotsy wrote. "Specific purity is indicated by the uniformity and identify of the F1 generations obtained by crossing the individuals to be tested, reciprocally" (Lotsy 1916, p. 23–24, as cited by Wilkins 2009). As Drummond notes, one of the foremost shortcomings of Lotsy's view of species as homozygous races was that it seemed unlikely that such genetic purity would frequently, if ever, occur in nature. Thus there existed a kind of fuzziness between the relatively coherent sub-specific units (*sensu* Jordan and De Vries), on the one hand, and the genotype as a fundamental unit of hereditary variation.

One attempt to clarify the fuzziness between the Jordanian-De Vriesian species and Mendelian genetics was made by Dutch geneticist Arend Lourends Hagedoorn (1885–1953) and medical doctor Anna Cornelia Hagedoorn (née Vorstheuvel La Brand), b.?–d.?) in 1921. The Hagedoorns' concept of species was based both on Mendelian genetics and on what contemporary scholars might call a "neutral" theory of evolution.

> A new species is a group of individuals originated from a limited number of plants or animals in some way isolated from the body of the species. Such a group must automatically become pure for its own type. The group can be said to constitute a new species, if the type is a new one, in other words if the total potential variability of the isolated group admitted of such a new set of genes. (Hagedoorn and Hagedoorn 1921, p. 201)

Here "potential variability" refers to the proportion of genes for which the group is not homozygous. The Hagedoorns postulated that such groups would be isolated by geographic or ecological factors, entailing a reduction in such variability purely by chance. Thus the isolated group would become differentiated in a variety of characters, and represent a new species. "Further, we believe that those individuals which are seen to differ in one striking

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point only from the members of a species in the midst of which they live, constitute a

variety," the Hagedoorns asserted, "whereas individuals differing in a group of characters

from hitherto described species — constitute a new species" (Hagedoorn and Hagedoorn

1921, p. 201–202). In their book, the Hagedoorns repeatedly reject the need to invoke

natural selection to explain the differentiation of isolated groups. Such differentiation was, in

their view, merely the continual elimination of variation by repeated isolation.[13]

In contrast to Lotsy and the Hagedoorns, Göte Turesson's concept of species was

characterized by an abundance of genetic variation rather than a lack of it. Turesson

postulated a theoretical entity that he called the *coenospecies*, which represented "the total sum

of possible combinations in a genotype compound" (Turesson 1922b, p. 345). The

coenospecies was comprised of all of the possible genotypes that would occur if there were

complete admixture within an *ecospecies*. The ecospecies was, on the other hand, the actual

instantiation of the coenospecies in nature: the genotypes distributed across the various

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[13] This focus on differentiation through loss of variation suggested that the hybridization of
such isolated groups—the Hagedoorns' species—played an important role in evolutionary
change, as it was the foremost mechanism by which variation could be increased. This was
a typical view at the time. The Hagedoorns thought that "a mutation can consist of either
the spontaneous acquisition of a gene, or of the spontaneous loss." (Hagedoorn &
Hagedoorn, 1921; p. 141) The Hagedoorns did retain a role for natural selection, but with
a notably probabilistic tinge.

> It is possible, that a group of organisms which is temporarily cut off from random
> crossing with the multitude, will become pure for a genotype which will afford the
> individuals having it a possibility to live in somewhat different conditions as
> compared with the related species. In other words, it is possible for a small group of
> organisms with a high potential variability, to come to fit into a different ecological
> niche. This, evidently, is what we should term natural selection.(Hagedoorn &
> Hagedoorn, 1921; p. 185)

In other words, natural selection is just the happenstance case that a group with
particularly well-suited genotypes are isolated in a new ecological context, and become
established therein.

habitats in which the coenospecies occurred. The ability of an ecospecies to persist in a variety of habitats, Turesson argued, was due to its ability to respond "genotypically" to those specific habitats, forming distinct habitat-types, or *ecotypes*.

> The mass of genetically different biotypes which make up the Linnean [sic] species do not distribute themselves indiscriminately over an area comprising different types of localities. The biotypes, on the contrary, are found in nature to be grouped into different types, each confined to a definite habitat. … These habitat types, or ecotypes in my own terminology, do not originate through sporadic variation preserved by chance isolation; they are, on the contrary, to be considered as products arising through the sorting and controlling effect of the habitat factors upon the heterogeneous species-population. (Turesson 1925, p. 11)

Turesson's account of ecotypes aligned with the Hagedoorns' concept of species in that both are specific to a locale, and that such groups are differentiated on the basis of multiple characters. Similar to the Hagedoorns, Turesson saw the formation of an ecotype as a narrowing of genetic variation—a "factor-depauperation" (Turesson 1925, p. 229)—but by natural selection rather than chance alone.

Turesson deviated from the Hagedoorns' in his understanding of how genetic variation and phenotypic differentiation were related. For the Hagedoorns, the isolation and differentiation of a particular species in similar habitats need not at all lead to similar sets of differentiated characters. After all, those characters would be the product of the happenstance co-occurrence of independent genes. But for Turesson, not only did he attribute the primary agency for differentiation to natural selection by the habitat, but he saw

the ecotype as more than the sum of the genotypes that happened to co-occur in a particular

locale. An ecotype could be identified across multiple instantiations of a given habitat.

For example, Turesson describes the distribution of narrowleaf hawkweed (*Hieracium*

umbellatum L.) along the west coast of Sweden:

> The controlling effect of environmental factors on the composition of a
>
> species-population is most clearly brought out in the cases where the
>
> reappearance of a distinct locality occasions the reappearance of the habitat
>
> type typical of that locality. The different *H. umbellatum* types furnish good
>
> evidence on this point. The alternation of sea-cliffs and shifting beach-dunes
>
> on the Swedish west-coast gives rise to a corresponding alternation of the
>
> bushy, broad-leaved sea-cliff type and the dune type. Wherever the *H.*
>
> *umbellatum* population on that coast strip has been investigated, the sea-cliff
>
> localities … have been found to harbour only the broad-leaved sea-cliff type.
>
> The beach dune localities investigated […], which alternate with the cliff
>
> localities, have conversely been found to harbour the dune type. (Turesson
>
> 1922b, p. 337)

The Hagedoorns would have attributed the recurrence of particular forms in similar habitats

to the migration, isolation, and differentiation (by sampling alone) of species. But Turesson

attributed such recurrence to similarity of selective pressures, and the ability of the species to

respond to those pressures by way of particular ecotypes. "I do not think that these findings

are consistent with the generally accepted migration theory," Turesson wrote. "The

differences observed, which must be considered quite non-essential to the existence of the

plant in the various dune localities, go to show that the dune type has on the contrary

become differentiated separately at different points, as a response on the part of the species-population to dune conditions" (Turesson 1922b, p.339).

According to Turesson, the ecotypic response of a coenospecies was more than just the persistence of individually advantageous genes in particular populations, but represented a more coherent and predictable product of gene combinations. Turesson wrote that, "The failure on the part of a certain ecotype, say oect. alpinus [of *Melandrium rubrum*, for example], to reappear when the habitat reappears is thus caused by the dropping out of the oect. alpinus-determining factors on the way to the alpine region of the Alp range" (Turesson 1925, p.229). Turesson saw the ecotype as distinct form that would be realized wherever one found a species growing in particular set of environmental conditions. That distinct form was the product of a whole host of genes working in concert. "It must be remembered," Turesson cautioned, "that it is the sum total of the genes, the 'Gesamtgenotypus' [of Johannsen], which doubtless determine the presence of absence of a certain form in a certain habitat" (Turesson 1922b, p. 334).

Turesson did not conceive of (eco)types as genetically pure. There is no indication that he saw the instantiations of the dune ecotype of hawkweed, for example, on each beach dune as being genetically identical. Indeed, Turesson criticized Lotsy's conflation of species with pure lines.

> It is also evident that purely genetical units do not cover the genecological. It
> is, however, interesting to see how the genotype-conception is reflected in
> the species-concepts recently propounded by some geneticists. The genetical
> analyses of Linnean [sic] species brought the proof of the constancy of the
> genotype, which then became the real unit in genetics, while the Linnean [sic]
> species, being an aggregate of individuals with different genotypical

construction, is still held to be a purely conventional conception. To transfer the species-concept to the pure line-concept on account of the constancy of the genotype, as is done by Lotsy, is at the same time to ignore the ecological side of the species problem, no matter what ideas Linnaeus had as to the cause of the diversity within his species. (Turesson 1923, p. 174).

In contrast to Lotsy, Turesson saw genetic variation as crucial for the persistence of species in the face of environmental heterogeneity. "Thanks to its genetically heterogeneous nature, the Linnaean species is able to cover a vast region by responding genotypically to a wide range of different habitats within the region," Turesson wrote. "It is by studying the phenomena of these responses and their resulting products that we should gain a knowledge of the origin of the genecological units" (Turesson 1923, p. 174).

Turesson noted that populations can show a certain degree of differentiation from a particular ecotype. For example, he recognized deviations from a beach-dune ecotype of *Melandrium* in coastal Sweden.

If the collections of leaves of [the beach-dune] type are examined, it is at once seen that the series from the various places exhibit considerable differences. While the series from the Sandhammar set fairly closely resembles the Halmstad set, important differences as to leaf shape are seen in the Falkenberg set. These individuals do not have the linear leaves typical of the first series, but have leaves which are much pointed and remarkably broad in their lower part. Even in the individuals with quite narrow leaves the characteristic leaf-base is always to be seen. Thus these leaves show resemblances both to the cliff-type (which has the leaves broadest in the

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lower half) and to the dune type at Halmstad and Sandhammar (which has

long and narrow leaves). Now when the Falkenberg dune population as a

whole shows these undoubtedly non-essential leaf-characteristics, the

assumption appears most reasonable that the type in question has become

locally differentiated from a mixed population of the cliff-type … and of the

dune type of the south. (Turesson 1922b, p. 338)

Yet even in areas where hybridization between two ecotypes was occurring, perhaps in an

area intermediate to two distinct habitats, Turesson still spoke of those two ecotypes as

conceptually separable.

The coherence of Turesson's ecotypes, in contrast to the Hagedoorns' species,

placed them closer to the Jordanon and the De Vriesian "elementary species" than to Lotsy's

pure-line species. One could say that Turesson was less of a "splitter," maintaining the rank

of species at more or less the same level of variation as the Linnaean species, but also

recognizing the ecological and evolutionary significance of smaller units— ecotypes—within

the species.

Thus, as a result of genotypical responses of the species-population to

different habitats, isolated units are formed with the species much in the

same way as contemplated by Jordan (1905) and Hagedoorn (1921).

However, to speak of such units as "species", as is done by these writers, is

largely to strip the ordinate species, as found in nature, of one of its most

characteristic qualities, viz. the ability to respond genotypically to a wide

range of different habitats with such units or habitat types, representing

various combinations of Mendelian factors. (Turesson 1922b, p. 342).

For example, in his discussion of ecotypes in *Solidago virgaurea*, Turesson identifies only four ecotypes: Alpine, Subalpine, Lowland, and West Coast. Those ecotypes were differentiated on the basis of several characters, including the shape of their leaves and the form of their inflorescences. Turesson's ecotypes were certainly mutable, but they were also coherent and distinct enough to be abstracted away from any one locally adapted population.

Drummond sided with the Turesson view that Linnaean species are dynamic, and lauded Turesson's genecological theory as well as his empirical results as building on the Hagedoorns' observations about local differentiation.

> In my own opinion, the implication that the Linnaean species may be a
> dynamic rather than a static unit is also to be welcomed, though most
> systematists will probably not agree with this view. Apart from the question
> of its ultimate value, the emergence—even if it be but for a time—of this
> fresh line of research is a development to be encouraged, because it provides
> a common meeting-ground for systematists, geneticists, and ecologists, three
> schools of workers who, if not professedly in separate camps, are at any rate
> prone to become so deeply immersed in their respective specialised branches
> of research as to be in danger of forgetting that they are all equally concerned
> in the solution of the age-long problem of the nature and origin of species.
> (Drummond 1926, p. 329).

Drummond's enthusiasm for Turesson's genecology was highly influential for the young Gregor. As I describe in the following section, Gregor's interpretation of Turesson's ideas evolved gradually during the 1930s and 1940s, generating a style of genecological research that would in turn shape Bradshaw's investigative pathway in the 1950s and 1960s.

1.2.2. Plantago maritima

Turesson's genecology was not merely a theoretical framework: it also provided a set of methods for investigating heritable variation in natural populations. The cornerstone of Turesson's work was the "common garden" experiment. A major challenge involved in studying the genetics of wild populations of plants was distinguishing those differences in phenotypic characters due to heredity from "modifications"—those due to environmental influences. According to Turesson, such a distinction could be made by planting representative samples of various plant populations in a single controlled environment. Over time, Turesson suggested, the differences among those samples that were due merely to environmental influence would fade away, and only heritable differences would remain.

Gregor's early genecological work started from Turesson's view that there was a linkage between particular habitats and particular sub-specific types, and he employed Gregor's common garden technique. In the 1920s, Gregor worked with Frederick Whalley Sansome (1902–1981) on a wide-ranging study of several agriculturally important grass species. Sansome received both his B.Sc. and Ph.D. from Edinburgh University, and started his work as First Assistant at Craigs House at about the same time that Gregor arrived.

In their first genecological study, starting around 1925, Gregor and Sansome collected samples of Lolium perenne, Dactylis glomerata, Phleum pratense, and Phleum alpinum from various sites around Scotland (Gregor and Sansome 1927). The geographic separation of their collection sites—in East Lothian, Forfashire (now Angus), Kincardineshire, and Berwickshire—ranged from one to one hundred miles. Those sites varied mainly in the extent of grazing and exposure to coastal winds and spray. They also included samples of commercial varieties in their analysis.
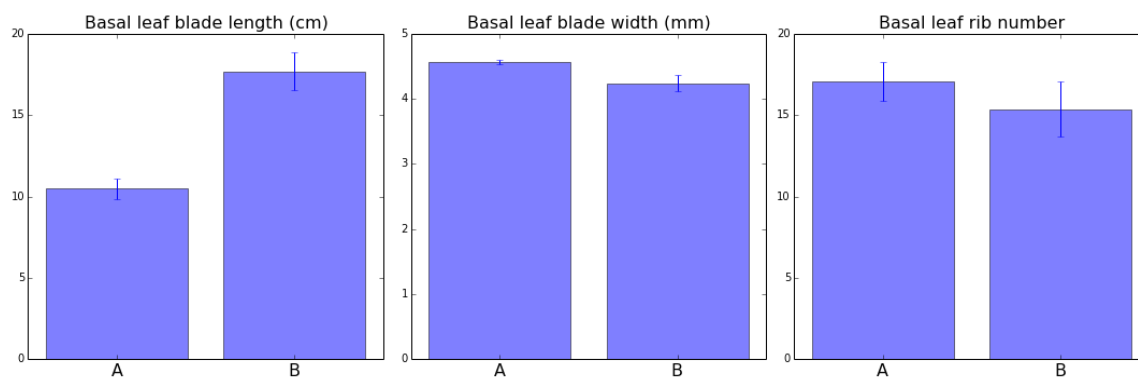
Figure 1.2.1. Differences in leaf morphology between two populations of *Lolium perenne*. Data plotted from table in Gregor & Sansome (1927). Error bars are variance in mean values for five blades on each plant. N=14.

To understand the sampling methods employed by Gregor, Sansome, and other genecologists who studied grasses, it is important to appreciate the anatomy of the grass plant itself. The typical grass plant has a single hollow or pith-filled stem, punctuated by solid swollen knuckle-like nodes from which the sheaths of the growing leaf emerges. The plant can spread by sending out above-ground lateral runners, called stolons, or by growing horizontal subterranean stem-like structures called rhizomes. New shoots called "tillers" can grow from the nodes of those stolons or rhizomes. Those tillers can form roots, and grow independently of the original plant.

Gregor and Sansome collected plants from the field, and brought them back to the experimental gardens at Corstorphine. The ability to grow plants from tillers, rather than from seed, made it considerably easier to sample grass populations, since far less time was required for the tiller to form an adult plant than if plants were grown from seed. Since the tillers of a plant are genetically identical, it also meant that multiple replicates of an experiment could be performed on the "same" plant. Thus they rooted multiple tillers of each plant in boxes in the greenhouse, and then planted them out in rows, forty inches apart and with 18 inches between plants. They then allowed the plants to grow for several years in

those uniform conditions, and periodically inspected various aspects of their morphology. At the same time, they performed crosses among some of the sampled plants to assess whether they were homozygous or heterozygous for various characters. For example, they measured the length, breadth, and number of ribs on plants sampled from different locales, as shown in figure 1.2.1.

Gregor and Sansome also surveyed populations of Timothy, *Phleum pratense*, a perennial grass considered important for grazing cattle (Gregor and Sansome 1930). In this and subsequent studies, Gregor and Sansome opted to collect seed samples rather than tillers due to the difficulty of transporting large quantities of vegetative material. There were also theoretical reasons to use seed. Gregor saw seed collections are more directly representative of the "genotypical composition" of a population. Moreover, plants grown from seed would
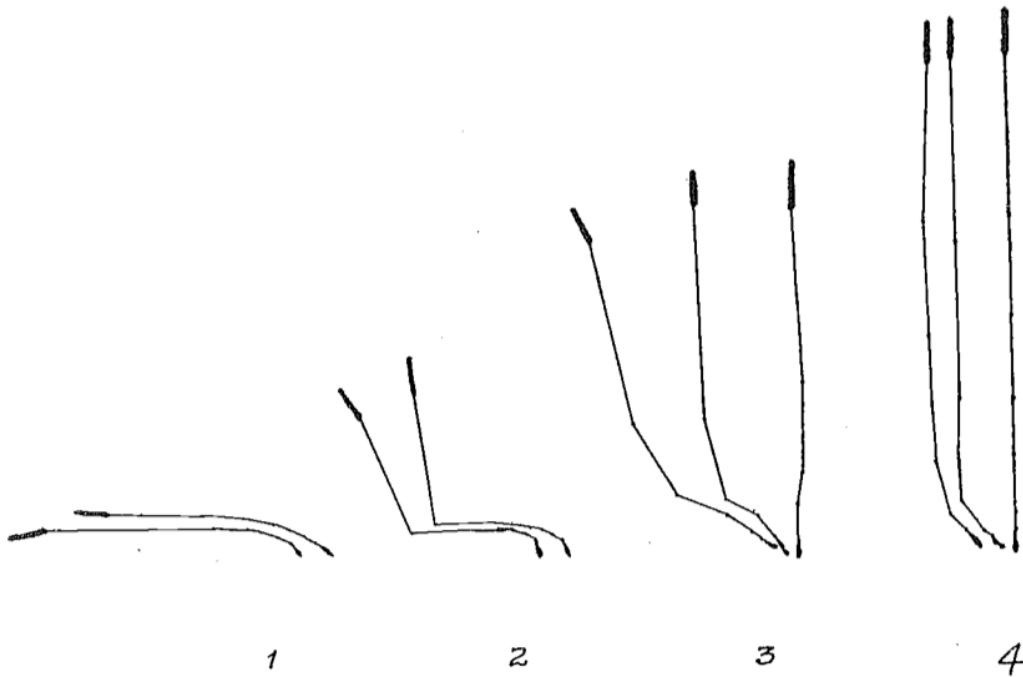
Figure 1.2.2. The four growth forms of *Phleum pratense*. (1) Prostrate, (2) decumbent, (3) ascending, and (4) erect. Fig 1 in Gregor and Sansome (1930).

develop entirely under uniform experimental conditions; there was no way to tell whether vegetative material was continuing to show environmentally-induced "modifications," or whether the effects of the environment in which they were found had worn off over time.

Gregor and Sansome sampled *Phleum* from a range of natural habitats, "waste places," and cultivated varieties. Once again, the plants were grown in greenhouses, planted out in rows (75 cm between rows, 45 cm between plants), and observed for two years. Their results indicated that there were two distinct "groups" within *P. pratense*: a "wild" hexaploid (2n =42) group, and an "American" or cultivated diploid (2n = 14) group better suited to drier conditions. They made a similar division in *P. alpinum* among Scottish tetraploids (2n = 28), which preferred moist habitats, and continental diploids (2n = 14) found in drier locales.

Figure 1.2.3. Sea plantain, *Plantago maritima*. Photograph at left by Cwmhiraeth [http://commons.wikimedia.org/wiki/User:Cwmhiraeth]. Licensed under CC-BY-SA-3.0 Unported and GNU FDL. Figure at right from Johann Georg Sturm (1796), public domain.
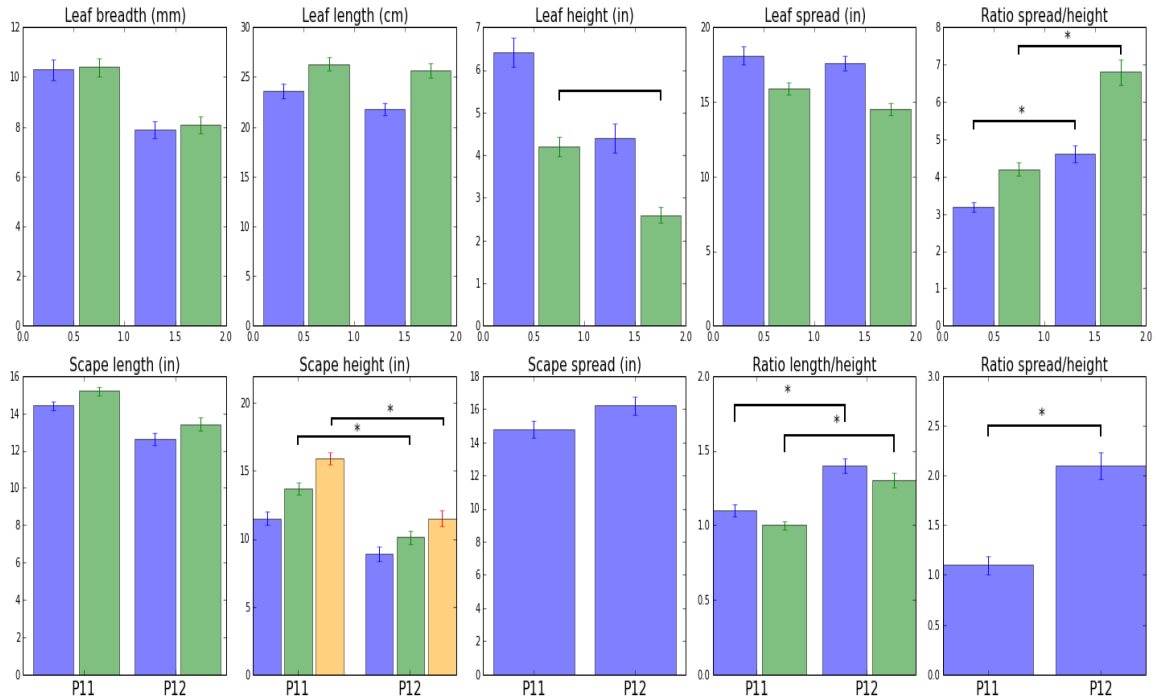
Figure 1.2.4. Differences in *Plantago maritima* sampled from two contrasting habitats on the east coast of Scotland. Horizontal bars indicate statistically significant differences in means. Blue, green, and orange bars represent the first, second, and third round of measurements for a given character. Data from Gregor (1930).

Gregor and Sansome further divided *P. pratense* according to four distinct growth habits: prostrate, decumbent, ascending, and erect (Figure 1.2.2).

Following Turesson's genecological system, Gregor (1931) proposed a taxonomic reorganization of the two species of *Phleum*. According to Gregor, the Linnaean species *P. alpinum* and *P. pratense* should be considered a single coenospecies, instantiated as four distinct ecospecies: *P. pratense diploidium*, *P. pratense hexaploidium*, *P. alpinum diploidium*, and *P. alpinum tetraploidium*. Each ecospecies would be further divided into several ecotypes corresponding to their growth habit. For example, *P. pratense diploidium prostratum*, *P. pratense hexaploidium erectum*, and so on.

In addition to his work with Sansome on grasses, Gregor also undertook a genecological study of sea plantains, *Plantago maritima*, in coastal environments (Figure 1.2.3).

It was Gregor's body of work in *P. maritima* for which he became most widely known. His first study of *P. maritima*, initiated in 1926, involved two closely adjacent habitats on the east coast of Scotland (Gregor 1930). *P. maritima* is an herbaceous perennial plant that is widely distributed along the coasts and salt-marshes of the Americas, Europe, North Africa, and northern and central Asia. The name of the genus, *Plantago*, is derived from the Latin word *planta*, sole of the foot, referring to its flat, fleshy leaves and low spreading growth habit. On the exposed red sandstone just beyond the reach of the tide, small, squat plants buffeted by sea breezes and salt spray grasped at the few pockets of soil trapped on precarious weathered ledges (population P12). Just above the rock, taller plants grew in far greater numbers on a grassy slope (population P11). Gregor collected seed from fifty individuals in each habitat, then sprouted and raised them under uniform conditions at Corstorphine, just as he had done with the grasses: sown in the greenhouse, transferred to boxes as seedlings, planted out in rows in the experimental garden, and watched closely for two years. The results from Gregor's (1930) *P. maritima* paper are plotted in figure 1.2.4. The salient differences that Gregor reported were in leaf and scape morphology, which contributed to an overall lower habit of growth in the P12 (sea cliff) population. Gregor's broader project on *P. maritima* went far beyond those two populations and included over thirty morphological and physiological characters.

Two aspects of Gregor's interpretation of Turessonian genecology are clear from his early writings. First, following Drummond, Gregor saw genecology as directly addressing taxonomic problems. Gregor argued that morphology alone, in the absence of ecological or genetic data, was a poor guide for classification. "The concept of Turesson," however, "appears ... to be a constructive attempt to place the groupings of organisms on a more natural basis" (Gregor 1931, p. 206). That was a view shared by others at the Scottish Plant

Breeding Station, including J. M. S. Lang, Gregor's research assistant from 1927 to 1942,[14] and geneticist V. M. Davey, who was tasked with making sense of commercial varieties of swede (turnip). In 1936, the three SPBS staffers articulated a vision for a taxonomic system focused on intraspecific variation that would operate in parallel to the existing traditional plant taxonomy:

> Experimental taxonomy fully appreciates the value of morphological differences—in fact the cytologist has disclosed a fresh field for such investigation—but it also seeks to show the causes which underlie those differences, and to ascertain their physiological, ecological, or genetic nature. The species unit of orthodox taxonomy often includes minor units, which exhibit various degrees of morphological differentiation, regardless of whether such degrees have similar biological significance. Experimental taxonomy, on the other hand, transfers the emphasis from the species unit to the local race…it is an attempt to classify evolutionary groups as they occur in Nature. On an extensive scale, as when the flora of a new region is being explored, the existing methods of taxonomy are undoubtedly those that would be employed. Experimental methods, however, would afford a means of probing more deeply into the nature of plant groups such as species of economic importance and others likely to yield valuable data relating to problems of evolution. A system of experimental taxonomy would make

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[14] Lang went on to work at the Ministry of Aircraft Production, starting in 1942 (GD449/7; letter from Gregor to unknown, 17 April, 1951).

readily available this detailed information to botanists studying the

phylogeny, distribution and ecology of plants. (Gregor *et al* 1936, p. 324)

Such an experimental taxonomic system would not replace traditional taxonomy, but

complement and extend it by providing concepts and methods better suited to classifying

intraspecific variation than, say, the morphological analysis of herbarium specimens.

Second, Gregor saw ecotypes as relatively distinct units, coherently delimitable on

the basis of multiple characters. "The ecotype concept postulates that the innumerable

character combinations become sorted out and grouped by the environment in virtue of the

constitution of the plant as a whole," Gregor wrote, "and not because of any phenotypic

character in particular" (Gregor *et al* 1936, p. 347). In contrast to the indicative, qualitative

characters on which taxonomists tended to base their discriminations, most of the characters

that Gregor considered in his work in *P. maritima* were continuous: individuals varied in

those characters by grades and degrees. "Qualitative and continuous characters assume

greater importance than qualitative and discontinuous in the differentiation of races of

'subspecific' rank," Gregor wrote, "Moreover, cognizance has to be taken of the different

combinations and proportions in which the same characters may appear locally under the

selective influence of the prevailing environment. The problem, therefore, becomes one of

assessing average character values and the significance of the differences between

ecologically distributed populations, rather than one of describing individual variations"

(Gregor *et al* 1936, p. 347). Indeed, in Gregor's early writings about *P. maritima*, his attentions

revolved first around whether heritable differences between contrasting populations could

be found at all, and second on characterizing differences among populations in terms of a

whole-organism adaptation to prevailing conditions.

It is worth noting the importance that Gregor placed on environmental "modification" (what later writers, including Bradshaw, would call "phenotypic plasticity") in his early papers. In his early studies in *Plantago*, Gregor (1930) noted that the phenotypic differences between the sea-cliff and pasture populations were much more pronounced in the field than in the experimental garden and, more importantly, the individuals within those populations were considerably more uniform in their appearance. While experimental cultivation yielded evidence that the two populations had different hereditary constitutions, what was causally significant for the survival of the sea cliff plants in their natural habitat was their ability to respond to the exposed conditions by forming a dwarf phenotype. Consistent with Turesson, Gregor allowed that the sea-cliff population had a variety of distinct genotypes—hence the greater degree of variation in the experimental garden than in the field—that persisted by virtue of their shared ability to form a particular adaptive phenotype in the habitat in which they occurred.

1.2.3. The Complementary Principle

Prior to and during World War I, an abundance of cheap feed for stock shifted land-use priorities away from maintaining grazable pasture-land and toward tilling for crop production. As the war drew to a close, however, the long-term problem of providing sustainable sources of protein for a growing British population raised concern about food security: the continued ability to import cheap feed was not guaranteed, and attention turned to re-establishing productive pastures. Thus the project of interwar pastureland restoration was characterized by three major problems: (1) bringing order to a chaotic and unregulated seed market, suffering from high levels of weed contamination and overall poor germination, (2) understanding the biotic and abiotic factors that influenced the establishment of reliable

and productive grasslands, and (3) establishing systems of stock and vegetation management that leveraged those grasslands in economically viable ways.

Gregor saw his work at the SPBS as part of a national effort to domesticate the Scottish cattle industry. "Even during the war period, with its transport difficulties, nearly half the store cattle fed off in Scotland were of imported origin," Gregor wrote, "If then the Scottish store cattle industry could be further developed on a small scale, in the more remote and mountainous districts dominated by natural and semi-natural grassland, it might have far-reaching effects upon the general farming economy, not only of the districts concerned but of Scotland as a whole" (GD449/6/282). In some parts of Britain there was a strong argument for simply reclaiming crop and waste-lands through the sowing and cultivation of high-quality forage plants. In the more remote regions of Scotland, however, this was not an economically viable strategy. Although such cultivation had been shown to lead to significant gains in carrying capacity during the summer months, few gains were possible during the winter. Many of the upland grazings were physically too difficult to manage in that way, and the rough terrain made it infeasible to harvest summer production for winter use.

In the 1940s, Gregor developed and championed a strategy for what he called "complementary" grazing. Rather than attempting to reclaim large areas of pasture, Gregor proposed cultivating smaller areas of high-protein pasture that would complement lower-quality uncultivated grazings. During the spring, these smaller pastures could be grazed until an adequate supply of vegetation had built up on the hillier pastures. When stock were moved into those more remote areas during the summer, the cultivated lowland pastures could produce hay and silage for use during the winter. Alternatively, smaller areas of high-quality pastureland might be cultivated directly adjacent to the rougher natural grazings, and

stock could be rotated—either voluntarily or by herding—between the cultivated and uncultivated areas.

Working out the details of how such a rotational "complementary" system could be successfully implemented was the overarching goal of Gregor's research from the late 1930s onward. This involved the subsidiary problems of selecting and managing appropriate varieties of herbage plants, and of correctly circulating stock on the grazings. Gregor undertook his first trial of the complementary grazing system in 1937, reseeding a two-acre area with high-quality herbage—*Dactylis glomerata* and *Trifolium repens* on one half, *Lolium perenne* and *T. repens* on the other—adjacent to a sixty-acre area of lower-quality uncultivated grazing. When the trail was run with Jerseys it seemed to fail miserably, as the protein-hungry dairy cows were fixated on the cultivated sward. A second attempt was more successful: when Gregor reran the trial with dry cows and heifers, the herd voluntarily balanced its time between the high-protein cultivated plots and the rougher pastures. The success of that second trial, however, created an additional problem: since the cattle spent more time on the rougher pasture, the amount of nitrogen available to plants in the reseeded sward dropped noticeably, which in turn impacted protein production and overall growth. That meant that additional nitrogen treatments were required for the cultivated sward. The overall problem of maintaining high protein production in cultivated pasture prompted Gregor to investigate the protein production of different varieties of herbage plants, and how those varieties responded to nitrogen treatments. Another problem was that the cultivated herbage needed to withstand a great deal of traffic by the stock, since the high-

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quality pasture was relatively small in relation to the quantity of cattle that would depend on it.[15]

The importance of high-protein forage grasses for Gregor's complementary grazing system prompted him to undertake a genecological study of perennial ryegrass, *Lolium perenne*, in the mid-1940s. The search involved both natural populations and commercial strains. Gregor described the rationale for that undertaking in a letter to James F. C. Hogg at Messrs David Bell, Ltd., a seed merchant in Dublin, written in 1945. "We are searching for a good mid-season ryegrass, and your material may well supply the type we are looking for. […] The object of our investigations, as you know, is to make more economical use of rough grazings adjoining ploughable land. So much of our rough pasture is unploughable and carries a vegetation which is not likely to give a reasonable response to manurial treatment. It seems, therefore, a much more practical proposition to cultivate small areas which can be ploughed, and to use them to produce high quality grass as complementary feed than to attempt wholesale hill-land reclamation" (GD449/4/90).

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[15] In 1945 Gregor established an experimental station at Dundonnell at which to carry out further experimental work on the complementary grazing system.

Most of the early legwork for Gregor's ryegrass work was carried out by Patricia J. Watson (Figure 1.2.5), a Ph.D. student from Glasgow. Watson came to botany somewhat later than her peers, beginning her graduate research in her late 30s or early 40s. She grew up in a very wealthy family in Glasgow, and attended the university there to study Classics (Harberd 2013). It is not entirely clear what prompted Watson to return to academe later on, but in 1945 she enrolled in the Ph.D. program at Glasgow, supervised by Gregor, and was

Figure 1.2.5. Patricia J. Watson, with David J. and Muriel Harberd's children. Courtesy of David J. Harberd.

awarded a scholarship from the Carnegie Trusts for the Universities of Scotland. Watson's Ph.D. research focused on the genecology of sheep's fescue, *Festuca ovina*, in relation to altitude. Watson sampled *F. ovina* from hillsides in two areas of the western Scottish highlands: Taynuilt, at the Pass of Brander, and Dalmally, about twelve miles to the east (GD449/4/111). She collected seeds at intervals of 50 feet in elevation, and set them out in a common garden trial back at the Scottish Plant Breeding Station.[16] Watson found a strong correlation between altitude and leaf length relative to leaf breadth at both Taynuilt and Dalmally (GD449/4/111).

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[16] In the course of this work she also examined the chromosomal cytology of the plants along that gradient, and found that there were two distinct chromosomal races present: a diploid race, and a tetraploid race. Watson was fascinated by the discovery, and undertook a far more ambitious project collecting *F. ovina* from a wide range of locales around Scotland, England, and Wales. She found that while all of the *F. ovina* from England and

Although Watson initially spent only her summers at the Station, she became an increasingly valuable part of the Herbage and Plant Genecology Section. In late 1946, well before she had completed her analysis and write-up of her dissertation, Gregor proposed to hire her on to carry out work on ryegrass. This led to an application to the Department of Agriculture for Scotland to fund the position. Instead of funding the ryegrass project in one grant, however, the DOAS divided the project into two parts to be completed in discontinuous years. The first part, the collection of ryegrass samples from around Cornwall, was to be funded in the 1946–1947 financial year, while the second part, the evaluation of the samples, was to take place in the 1948–1949 financial year (GD449/4/101). Gregor and Mr. William Robb, the Director of the SPBS, worked out an arrangement in which the funding for the first phase could pay for a temporary assistantship—four months in length—that could support Watson until a more permanent position could be developed (GD449/4/102). Watson accepted the offer and, in the spring of 1947, traveled extensively in the southwest of England, collecting samples of ryegrass from a very large number of sites in Devon, Cornwall, and the Scilly Isles.

Meanwhile, Gregor continued to pursue funding for the project. In February, 1947, Gregor was invited by Sir John C. F. Fryer at the Agricultural Research Council to participate in informal talks among "those interested in research on grassland ecology" in London. Among the topics of interest was Gregor's proposals for expanding research on the genecology of grasses at the SPBS. At the meeting, Fryer expressed interest in the ryegrass

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Wales were diploid, and that the tetraploids found in Scotland only seemed to occur on more fertile soils, the diploids in contrast occurring in poorer, more highly acidic soils.

project, and two weeks later Gregor followed up with a letter spelling out the project in greater detail. Once again, Gregor outlined the logic of his complementary system of grazing.

> For some years past we have been endeavouring to find a means of augmenting the diet of hill stock with highly nutritious grass in order to correct the evil effects of malnutrition commonly associated with the districts of very high rainfall. If, however, we are to use the very limited ploughable area…to raise the nutritional standard of hill stock, not only must large numbers of animals be given access to the cultivated grass, but such grass must be made to supply in the highest possible degree the nutrients which the hill vegetation lacks. In other words, the small area of cultivated grass will have to be used as the nutritional complement of a much larger area of rough herbage, and of the breeding stock in particular, at the correct season of the year. (GD449/4/85).

The success of this system, Gregor explained, depended on choosing strains of grasses that could form a dense sward, withstand treading, and produce highly nutritious growth at the correct times of the year. The logical strategy for identifying those strains, Gregor argued, was a genecological research program:

> Although certain late varieties of ryegrass combine dense growth-habit with high yields the desirable combination has so far not been found among any of the early varieties at present on the market. However, certain samples of ryegrass from old pastures in Devon have been found to contain types closely approaching what is wanted, though it remains to be seen whether such types are physiologically capable of high production in a more northern latitude. There are nevertheless good grounds for supposing that the naturally selected regional race…the local populations within a climatic region, could be used directly as commercial material

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provided suitable parent populations could be located and their breeding

potentialities tested. The success of certain ryegrass populations from long-

established pastures in the south-west of England under the environment of north-

west Scotland indicates that in this part of England there still exist some ecotypic

races which, for complementary purposes in the wet and mild districts of Scotland,

are equal in value to any bred strain yet produced. The war has been responsible for

reducing the area of old-established grassland and this makes a critical genecological

survey of the sources still remaining all the more urgent. Such surveys might well be

extended to cover other environmental regions and a number of other grassland

species, for it is quite evident that comparatively little is known of the ecotypic

variation occurring even within the major environmental regions of Britain, far less

within the agronomic sub-division of the different climatic environments

(GD449/4/85).

Gregor went on to justify genecological investigations in terms of both its practical and its

theoretical value.

The study of the distribution of ecotypic variation is of fundamental interest not

only to the practical plant breeder, but to the ecologist, and to all those who

undertake vegetational surveys, for while the taxonomic species has up till now been

generally accepted as the ultimate ecological unit it would seem likely that specific

tolerance to differences in environment is in large measure a reflection of the degree

of ecotypic differentiation within the taxonomic species. Recent work on *Poa* in

America, *Medicago* in Russia and *Festuca* in Scotland only emphasises the practical

implications of critical genecological investigations, and makes one wonder whether

too much stress is not being laid on the building up of a limited number of bred

strains mainly on the basis of morphological criteria and too little on the

physiological attributes which have accumulated under the influence of ecotypic

selection.(GD449/4/85)

The three examples of compelling genecological research that Gregor cited in the passage

above are those due to Jens Clausen in California (*Poa*), E. J. Sinskaja in Russia (*Medicago*),

and Watson's own dissertation research on *Festuca*.

Gregor's proposal to Fryer and the A.R.C. was two-fold. First, Gregor wanted to

create a full-time genecologist position. Gregor wrote that such a position would "continue

and extend the investigations relating to the geographical distribution of hereditary variation

within species and, in particular, to the ecotypic structure of species, upon which I was

engaged before the war" (GD449/4/85). Gregor intended that such a genecologist would

expand the scope of that work even beyond Britain. Second, Gregor requested that Watson

be appointed as permanent staff at the SPBS to oversee work on the genecology of ryegrass,

rather than creating a year-long position in the 1948–1949 budget.

> Since the beginning of this year we have acquired the services of a graduate worker
>
> on a temporary basis to collect and study the ryegrass populations of Devon,
>
> Cornwall and the Scilly isles. Incidentally this work will include an examination of
>
> the variability and characteristics of populations which are regarded by the Devon
>
> Seed Growers' Association as possible sources of Devon Eaver Stock-seed. … I
>
> therefore feel that in order to carry out the curtailed ecological programme, instead
>
> of creating a new post the temporary assistant who is at present in charge of the
>
> regional race survey should be transferred to the graded staff. (GD449/4/85).

Such an arrangement would free up funds to pay a chemist to perform nitrogen analyses on

the ryegrass races throughout the year.

The A.R.C. approved Gregor's request to appoint Watson as permanent staff, and to create a new position for a genecologist in the 1948–1949 budget. Watson and Gregor worked closely together on the ryegrass project, which was expanded to include populations in Scotland.

> At the Plant Breeding Station the perennial ryegrass of S.W. England is being examined in order to supply the local seed-growers' associations with the information needed for the multiplication of useful and reliable certified stocks. In view of the importance of Ayrshire perennial ryegrass to Scottish agriculture it has been decided, with the approval of the Grassland Improvement Committee, to conduct a similar survey of this regional race. Material for the study is being collected now and it should be available for examination during the summer of 1950. Running concurrently with these ryegrass studies is the investigation of the more academic aspects of population genetics, and especially of the ecological distribution of hereditary variation and its classification. (Report on grassland investigations conducted by the Scottish Plant Breeding Station, to the Scottish Agricultural Advisory Council Grassland Subcommittee, 17 December 1948; GD449/6/285)

Unfortunately for Watson, her dissertation was somewhat delayed by the enormous work involved in the ryegrass research. Those delays were compounded by serious injuries in the summer of 1948 that left her bedridden in the hospital for several weeks, and unable to conduct fieldwork for an extended period thereafter. Ultimately, Watson received her Ph.D. from the University of Glasgow in 1950, with recommendations from Gregor and from D. H. Valentine, her external reader.

When Bradshaw wrote to Gregor in the summer of 1948, then, the immediate research goals in the Herbage and Genecology Section were twofold: (1) the efficacy of nitrogen treatments for raising protein content in various herbage plants, and (2) an extended genecological surveys of perennial ryegrass in in Britain. More importantly, Gregor was eager to fill his newly-funded genecologist position.

1.2.4. Ecotypes and Ecotypic Differentiation

During the 1940s, Gregor's views on the nature of ecotypes and aims and practice of genecology underwent a gradual but significant shift. Those changes were foreshadowed by two aspects of Gregor's methodology: the scale on which he sampled plant populations, and his attention to continuous variation. By the late 1940s Gregor had abandoned the idea that genecology could or should inform taxonomy. Moreover, he had moved away from a conception of ecotypes as discrete habitat-specific units delimitable on the basis of multiple characters. Gregor argued that genecologists should not spend their time attempting to distinguish discrete ecotypes, but rather focus on describing patterns of differentiation in individual characters in relation to gradients in specific environmental factors.
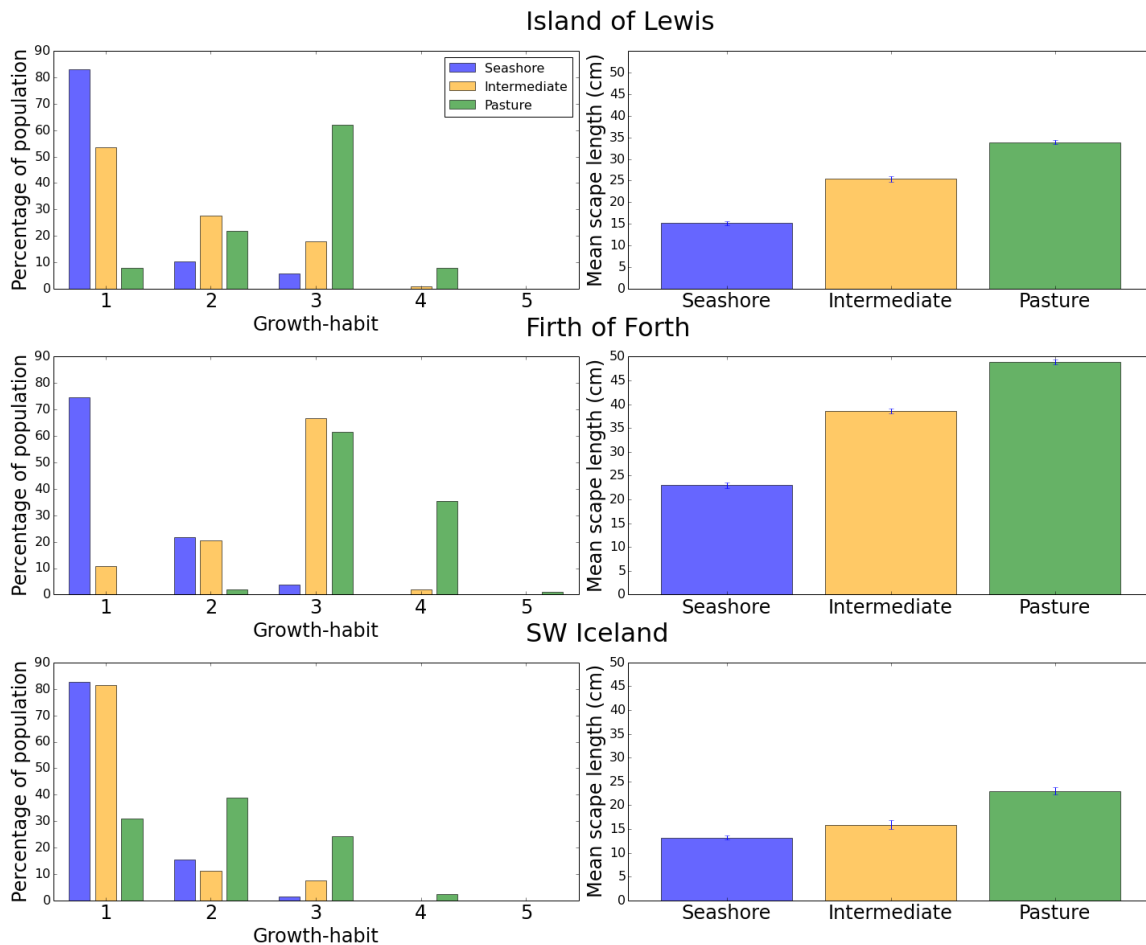
Figure 1.2.6. Distribution of growth forms of *P. maritima* in population samples along edaphic gradients in three locales. Growth habit (left panels) ranges from prostrate (1) to upright (5). Mean scape length (right panels) is consistently higher in samples from pasture than in the saltier soils near the seashore. Data from Table 2 in Gregor (1946).

One of the causes of this gradual transformation in Gregor's thinking about ecotypes was his early decision to sample populations on relatively small spatial scales. Recall that Gregor's earliest work on *Plantago maritima* involved populations that were almost immediately adjacent to each other: a rocky outcrop just above the high tide line, and a grassy hillside just above it. In section 1.2.3, I mentioned that Watson's sampling stations in the western highlands were spaced at vertical intervals of 50 feet.

Such small-scale sampling remained characteristic of Gregor's genecological research. Around 1937 Gregor had sampled *P. maritima* from the island of Lewis, in the northern Hebrides, from the Firth of Forth in Edinburgh Bay, and from southwestern Iceland, along what he considered to be similar edaphic gradients. At each of the two sites in Scotland he sampled from three areas: the salty mud at the water's edge, fertile meadows well above the high tide mark, and an area approximately halfway between the two extremes. At the Iceland site, he sampled from the rock wall of a hot spring, an area intermediate to two springs, and in a pasture nearby. As in the results presented in his 1930 paper, Gregor focused largely on differences in growth habit and size. Gregor found that the populations at each site did vary in growth habit, but that this was a matter of quantitative differences in the relative representation of growth habits (Figure 1.2.6). The differences in representation of growth habits were accompanied with differences in overall plant size, indicated by scape length. So although there were clearly ecotypic differences among the populations—a clear genotypic response to differences in habitat—those differences were better characterized in terms of a gradation of differentiation than in terms of discrete ecotypes.

Indeed, by the mid-1940s, Gregor's concept of ecotype had broadened considerably, no longer emphasizing differentiation with respect to multiple characters.

> It should perhaps be emphasized that the ecotype concept … embraces all intra-ecospecific variation of ecological significance, the term 'ecotype' being applicable to any population differentiated in respect of any characteristic attributable to the selective action of ecological factors. (Gregor 1946, p. 267).

Gregor advocated the use of Julian Huxley's (1938) "cline" terminology to describe the kind of ecotypic differentiation that he observed in *P. maritima*, and that he suggested was likely widespread in nature; rather than identifying eco*types*, Gregor suggested that greater attention

be given to describing eco*clines*—continuous gradations of ecotypic differentiation across an environmental gradient. "Tuesson considers ecotypes to be recongisably discontinuous variational units," Gregor wrote, "and that his treatment is not concerned with the ecological trends of character variation" (Gregor 1947, p. 380). Cases in which an ecotype was named and delimited, Gregor asserted, would most often turn out to be merely a demarcated region along a continuous ecocline, "a subjective reference range of variation" (Gregor 1947, p. 387).

Gregor further clarified his conception of ecotype around this time in a letter to Elisabeth Schiemann at the Kaiser Wilhelm Institute for Kulturpflanzenforschung, in Berlin.

> Turesson's ecotypes are, as you well know, objectively definable habitat populations, whereas my idea of an ecoclinal ecotype is that of a subjectively delimited range of ecotypic variation. … It is true that Turesson's concept has more general application, because his term ecotype could I feel sure be appropriately applied, in theory at least, to most, if not every, areal population, for every one must be tolerant of, and in some respect adapted to, its environment in order to survive at all. The difficulty arises when one tries to describe the nature of this adaptation to the total habitat environment. It would for example, be impracticable to delimit as discrete individual ecotypes all the slightly differing populations of Red Clover which contribute to the Late-Early variational trend which is associated with the South-North agro-ecological gradient in Western Europe. … instead of trying to delimit a host of areal ecotypes, efforts should be directed towards recording the general trends of variation by relating ecotypic character variation to particular agro-ecological gradients.

Those patterns of ecotypic character variation would likely intergrade and overlap in complex ways, Gregor thought, so that attempting to delimit discrete ecotypes on the basis of any one of those characters would be arbitrary at best.

By the end of the 1940s, Gregor no longer saw genecology as a taxonomic project. In a letter to a colleague at Glasgow University, Gregor wrote, "Personally I think that in proposing new terms we should aim at presenting ideas, in condensed form, backed by experimental evidence rather than creating taxonomic categories more or less rigidly fixed by practical needs. The significance of the ecotype when used as a taxonomic category is practically nil, yet the ecotype as an abstract concept provides the working basis for a better understanding of bio-geographical and evolutionary problems" (GD449/7/114).

1.2.5. *The Californian Tradition*

The significance of Gregor's small-scale sampling for his conception of ecotypes is brought into better relief when contrasted with the work of Gregor's friend Jens Clausen (1891–1969), and Clausen's collaborators David D. Keck (1903–1995) and William Hiesey (1903–1998), in California. Whereas Clausen and his colleagues focused on large-scale climatic differences between site separated by hundreds of miles, Gregor's populations were barely a stone's-throw apart, and their habitats differed primarily in terms of edaphic properties, particularly in concentrations of sea salts. The Californian ecotype was a clearly distinguishable unit of variation, such that members of that ecotype could be individuated in areas where their ranges overlapped. Indeed, their ecotypes were often synonymous with recognized subspecies. For Gregor, even in the early years of research, such a situation was conceptually impossible.

Smocovotis (1988) offers a detailed account of the work by Clausen and other California botanists during this period. Clausen was hired by Harvey Monroe Hall in 1931 to work as a cytologist in his team at the Carnegie Institution of Washington, in Stanford California. A native of Denmark, Clausen attended the University of Copenhagen where, at the suggestion of systematist Christian Raunkier (1860–1938) he undertook an investigation of the cytology of species in the Violacea (pansies). Clausen went on to work as an assistant professor at the Royal Agricultural College in Copenhagen in the early 1920s. During this period Clausen established close ties with Turesson who lived nearby in Lund, Sweden. In the late 1920s Clausen spent a year at the University of California at Berkeley, funded by a fellowship from the Rockefeller Foundation, and became well known within the California botany community for his work on the systematics of *Viola*. Due to Hall's untimely death in 1932, Clausen assumed leadership of the research team in Hall's lab.

Gregor and Clausen maintained regular correspondence at least as early as the 1940s, although there is some indication that their friendship had begun somewhat earlier. Gregor and Clausen cooperated (along with Turesson, and Paul Solberg in Norbu) on a multi-continental study of ecotypic differentiation in Kentucky bluegrass, *Poa pratensis*, after Gregor expressed interest in the possibility of testing some American varieties in Scotland as part of his complementary grazing scheme.

> We have been looking, with little success, for a winter-active grass for cultivation in the relatively mild climate of our west coast. We could make very good use of a grass which could be sown in July, grazed during the winter and early spring and ploughed up in time for the land to be reseeded again in July. We don't worry about persistence so long as we can get rapid establishment and plenty of growth. At the moment we are using *Lolium italicum* for this purpose and while it is capable under

prevailing environment of giving satisfactory grazing during the early part of the winter it can't meet the requirements of the grazing animal in January and February. (GD449/4/72).

Gregor and Watson cultivated several of Clausen's population samples at the SPBS, at least one of which seemed promising to Gregor as a cultivar in Scotland. "From the strictly agricultural standpoint the most outstanding performance under our conditions is that of the *P. pratensis* population from Oregon (4466-1);" Gregor wrote, several years later, "it is a type which might well be a useful constituent of permanent pasture in this country. Population 4559-2 might also have an agricultural value here on account of its ability to remain green during the winter" (GD449/6/136). Clausen visited the SPBS several times in the late 1940s and 1950s, and Gregor and Clausen exchanged personal letters regularly.

At the Carnegie Institution, Clausen inherited a research program that Hall had been developing for over two decades. Hall shared Turesson's interest in an integrative and experimental approach to plant taxonomy, and had developed a distinct but complementary investigative approach. Whereas Turesson focused on growing population samples in a single controlled environment, the so-called "common garden," Hall had developed a "reciprocal transplant" technique in which population samples were grown in a series of contrasting environments. Reciprocal transplants shed light not only on the extent of hereditary differentiation among plant populations, but also on the range of reactions of hereditary types to environmental conditions.

During the 1930s and 1940s, Clausen, Keck, and Hiesey became internationally known for their application of the reciprocal transplant technique to a variety of plant species in coastal California. Their best-known experiments involved sampling populations of tarweed (*Hemizonia angustifolia*), tidy-tip (*Layia platyglossa*), sticky cinquefoil (*Potentilla*

glandulosa), and a variety of other species from a series of stations along an altitudinal gradient in the Sierra Nevada (Clausen *et al* 1947). The lowest station was on the Stanford campus, 100 feet above sea level, and the highest was a site known as "Timberline," around 11,000 feet, in more arid conditions east of the ridge of the Sierra Nevada range. The main premise of those experiments was that ecotypes that might be indistinguishable in one environment might exhibit dramatic differences when grown in a contrasting environment. Moreover, the severity of a race's response to a contrasting environment might provide some indication of the extent to which that variety was specially adapted to its habitat.

Whereas Gregor's populations of *P. maritima* were within sight of each other, or even directly adjacent, the Carnegie team's field sites at Stanford and Timberline were more than 200 miles apart. Correspondingly, their conception of ecotype emphasized strong discontinuities in multiple characters. In *Potentilla glandulosa*, for example, Clausen, Keck, and Hiesey (1941) recognized five distinct ecotypes distributed from near sea level to the top of the Sierra Nevada:

1. The Coast Range ecotype, sampled at 600 feet, ranging from 600 to 5,000 feet;

2. The Sierran foothill ecotype, sampled from 2,500 feet, ranging from 700 to 6,800 feet;

3. The mid-Sierran meadow ecotype, sampled at 4,600 feet, ranging above 4,000 feet;

4. The subalpine ecotype, sampled at 5,800 feet, ranging from 5,000 to 8,000 feet;

5. The alpine ecotype, sampled at 10,000 feet, ranging from 7,500 to 11,000 feet.

Those five ecotypes were differentiated on the basis of many morphological, physiological, and reproductive characters—e.g. growth form, timing of flowering, morphology of reproductive structures. Clausen *et al.* (1941) noted that, where they overlapped, their five ecotypes could form viable hybrids, and thus belonged to the same species.

The differences in the conceptions of ecotypic differentiation held by Gregor and Clausen become clearer when one considers how Gregor might have approached the ecotypic differentiation in *P. glandulosa* in the Sierra Nevada. For Clausen, it made sense to distinguish a Sierran foothill ecotype and a Coast Range ecotype growing in the same area at, say, 2,500 feet. In contrast, even in the early 1930s Gregor would have described a single ecotype at 2,500 feet, characterized by specific proportions of distinct growth forms. Gregor (1947) noted that Clausen's five ecotypes of *P. glandulosa* corresponding almost precisely to traditional taxonomic subspecies: the Coast Range corresponding to ssp. *typica*, the Sierran to ssp *reflexa*, the mid-Sierran to ssp *Hanseni*, and the subalpine and alpine ecotypes to ssp *nevadensis* (Clausen *et al* 1941). By the mid-1940s, Gregor thought that the ecotypic trends found by the Carnegie trio should not be described in terms of separable ecotypes at all, but instead be described in terms of variational trends in individual characters in response to patterns of climate and soil.

Another important difference between Gregor and Clausen was the nature of the environmental differences on which they focused. Whereas Clausen and his team were interested in climatic differences due to the dramatic topographic variation of western North America, Gregor's primary concern was adaptation to different soil types. For example, Gregor's environmental gradients in his work on *P. maritima* in the 1930s were essentially differences in soil salinity due to varying proximity to the seashore. That difference in emphasis was highlighted in an exchange between Gregor and another California botanist, Arthur R. Kruckeberg (1920–), in the late 1940s.

Kruckeberg had worked as a field assistant for Clausen after graduating from Occidental College in 1941, and after a stint in the Navy during WWII enrolled in the Ph.D. program at Berkeley in 1946 (Olmstead 2007). Kruckeberg's dissertation research, supervised

by Herbert Mason, focused on the effects of serpentine soils—volcanic soils characterized by a low calcium-to-magnesium ratio, a paucity of essential nutrients, and toxically high levels of heavy metals such as chromium and nickel. In several cases, Kruckeberg had found populations of plants that appeared to be specially adapted to the serpentine soils. In the summer of 1949, Kruckeberg reached out to Gregor for input. "It appears that of the many researches on the nature of the ecotype," Kruckeberg wrote, "yours is just about the only work to touch upon that important phase of habitat preference, the edaphic factor. Here in California where the opportunity for the study of ecotypic differentiation on the vast array of soil types is ideal, it seems that the climatic phase of ecotypic elaboration has been the chief object of research" (GD449/6/387). In his reply, Gregor reiterated his views on the genecological research agenda. "From the standpoint of classifying ecotypic differentiation is appears as if we shall have to endeavour to relate particular ecotypic trends to particular environmental gradients," Gregor wrote, "your recognition of edaphic ecotypic differentiation is therefore of very real interest in this connection" (GD449/6/387). Gregor suggested that the paucity of work on edaphic differentiation was due partly to a lack of attention to physiological characters. "Differentiation in response to edaphic factors seems hardly to have been touched," Gregor wrote, "but perhaps when it becomes more common to study physiological attributes it will be found that edaphic differentiation is not so rare after all" (GD449/6/387).

As I describe in chapter 2, these differences between the Gregorian and Californian genecological traditions would resurface in the mid-1950s as Bradshaw sought to make sense of his own genecological investigations.

1.3. Detour

1.3.1. A Suitable Trainee

Under normal circumstances Gregor would not have so quickly agreed to accept Bradshaw as a Ph.D. student at the SPBS, having never met the man in person and having exchanged only a few letters. As part of his proposal to the Agricultural Research Council concerning the ryegrass project, Gregor successfully argued for the establishment of a full-time genecologist position in the Herbage and Genecology Section at the Scottish Plant Breeding Station, starting with the 1948–1949 budget year. After a campaign of letter writing to solicit the position, however, Gregor found it more difficult than he had anticipated to find a suitable candidate. So when Bradshaw wrote to Gregor in the spring of 1948, from Gregor's perspective, Bradshaw's interest could not have been more timely. As Gregor confided to Sir John Fryer, Secretary of the A.R.C., "I might mention that after some searching we had reached the conclusion that to get a suitably trained Genecologist our best plan was to find someone interested in this line of work and train him ourselves — Bradshaw seems to us to be a suitable trainee" (GD449/6/205). Given the impending deadline for Bradshaw's proposal to the A.R.C. for a graduate studentship, Gregor agreed to take Bradshaw on.

Bradshaw's mentors at Cambridge advised him to consider working in grasses, given their perceived importance in the post-war agricultural economy. Surprisingly, Gregor initially resisted this idea, apparently believing that the material would prove too difficult as a starting project for the young botanist. Gregor thought that too much of the ecotypic differentiation in grasses was due to "morphologically little-differentiated polyploid races" (GD449/5/8), and that grasses would simply be too difficult for Bradshaw to work with, at least to start.

Grasses, though certainly interesting from the economic as well as the

ecological standpoint, don't provide particularly easy material, and I would

suggest that in starting work of this kind it would be wise to choose a plant

easier to cross, measure and cultivate. Of course a grass could be tackled at

the same time, especially the preliminary cytological survey required to

establish the presence of any polyploid races. (GD449/5/8)

Yet Bradshaw remained committed to the idea of working with grasses. Bradshaw

replied enthusiastically to Gregor's synopsis, side-stepping the question of whether

grasses were suitable for a Ph.D. project.

I do agree that more information about the ecological tolerances of

taxonomic species is required. From what I have already seen it is very plain

how varied and separate can be the environments in which many species live,

which leads one to think that they are made up of several ecotypes.

(GD449/5/7)

Capitulating to Bradshaw's interest in grasses, Gregor suggested a provisional title for

Bradshaw's dissertation—"The distribution of hereditary variation in some components of

grassland vegetation with particular reference to the bearing of genecological and ecological

studies on problems of plant geography"—that "wouldn't confine [Bradshaw] exclusively to

grasses" (GD449/5/6). Following Gregor's suggestions, Bradshaw submitted his proposal

for a genecological project to the A.R.C.. Bradshaw's enthusiasm for this new direction of

research was unmistakable. At the May, 1948, Natural History Society Conversazione,

Bradshaw reported on a new "ecotype" of velvet bentgrass, *Agrostis canina*, in the mossy

areas of the Norfolk Broads. In July, Bradshaw traveled to Edinburgh to meet with Gregor

and the SPBS staff, and over the course of three days he and Gregor mapped out in greater

detail a plan of campaign for Ph.D. project focused on the genecology of bentgrass, *Agrostis

tenuis*.

That August, however, saw an unexpected turn of events. On August 6, Bradshaw

wrote to Gregor with mixed news.

> Dear Dr. Gregor, This is a sad letter that I have to write. I have delayed thanking
>
> you for the very pleasant stay I had, until I heard from the A.R.C. I have now heard
>
> that I have got my studentship all right. But they are sending me to Aberystwyth to
>
> work under Dr P. T. Thomas. Why there is the change I do not know. All I can say
>
> is that I think that it is a bit hard to be told coldly by the A.R.C that other
>
> arrangements have been made. It is disappointing especially because of the time I
>
> had with you a fortnight ago. (GD449/6/80)

Bradshaw's regret at the A.R.C. decision was palpable. Robert Crocker noted how excited

Bradshaw had been about going to Edinburgh, and shared Bradshaw and Gregor's

disappointment. "I saw Bradshaw shortly after his trip to Edinburgh and he seemed very

thrilled with the prospect of working there," Crocker wrote to Gregor that summer, "I saw

him again a few days later, and he told me he had been given a grant to go to Aberystwyth! I

didn't leave him in two minds as to how unfortunate I thought he had been"

(GD449/6/151).

Gregor was disappointed by the A.R.C.'s decision, yet he was not wholly opposed to

the idea of Bradshaw working with Thomas:

> Although I am naturally very disappointed that our plans for the next three
>
> years have gone astray, yet I feel that the A.R.C. "direction" has its

compensations. In experimentation of the kind we discussed a good working knowledge of cytology is a valuable acquisition since the first step in experimental taxonomic investigations is the delimitation of ecospecies which so often involves the determination of the interrleationships of cytological groupings. A training with a good cytologist like Thomas should give you just the kind of cytological background needed for the new approach to ecological problems. (GD449/6/83).

Gregor held out hope that, when Bradshaw had "absorbed Thomas' training" Bradshaw would be "'re-directed' to [the SPBS] to take up the study of the distribution of ecotypic differentiation" (GD449/6/83).

The fact that Bradshaw would not be working at the SPBS created an administrative dilemma for Gregor. In anticipation of Bradshaw's arrival that fall, he had asked Fryer at the A.R.C. to postpone allocation of funds for the genecologist position, and omitted the position from the budget for 1948. "Until we know what the intention [of the A.R.C.] really is we in Edinburgh are in a somewhat difficult position," Gregor wrote to Bradshaw, "for on the assumption that we would have you here for the next three years we withdrew an application to the A.R.C. for a genecologist. You know our accommodation is strictly limited and that we couldn't cope adequately with two new people and in particular with two additional lots of experimental material."(GD449/6/84). Gregor asked Bradshaw to consult with Professor Brooks to get a better sense of the A.R.C.'s plans, and whether it would be possible to attend the SPBS after a period at the WPBS. "Should there be a reasonable prospect of your being given the opportunity of coming to us after a period with Thomas we shall not for the time being ask the A.R.C. for a genecologist," Gregor wrote, "If, however,

the entire 3 year period of your studentship is to be spent at Aberystwyth then we shall in all probability revert to your original plan and look for a genecologist now" (GD449/6/84).

Bradshaw was advised that he was to remain at Aberystwyth for the full three years of his Ph.D. program. He continued to cultivate a relationship with Gregor, however, and the senior ecologist remained an important influence as Bradshaw articulated his own research program.

1.3.2. The Stapledonian Paradigm

The A.R.C. directed Bradshaw to work under the supervision of a cytologist, Percy Tudor Thomas (1910-1997). Just as the A.R.C.'s reasons for to sending Bradshaw to Aberystwyth were never fully explained, the decision to pair Bradshaw with a cytologist was equally mysterious. Thomas had himself conducted his graduate work at Aberystwyth, where he was greatly influenced by Sir Reginald George Stapledon, the inaugural director of the WPBS. After completing his dissertation on the chromosomal cytology of ryegrass, *Lolium spp*, Thomas accepted a position at the John Innes Horticultural Institute at Merton, where he interacted with geneticists Cyril D. Darlington, J. B. S. Haldane, Kenneth Mather, and Dan Lewis. Thomas was hired as Senior Lecturer at Aberystwyth just two years prior to Bradshaw's arrival, and was quickly promoted to Professor of Agricultural Botany at UCW (Rees 1997). Bradshaw thought the pairing with Thomas a "curious" one in light of his own ambivalence toward cytology, but found his supervisor to be not only a delightful person, but also reasonably permissive with respect to Bradshaw's research activities (D1041/13/2/9).

When Bradshaw arrived at the WPBS in September of 1948, the research agenda of the WPBS was dominated by the agricultural-economic vision of Stapledon and his long-

time colleague T. J. Jenkin. That vision, and the methods employed by WPBS staffers, were

tightly linked to genecological research.

In section 1.2.3 I mentioned the perceived significance of developing productive

pastureland for the economic and food security of Britain after World War I. This involved

reforming the chaotic seed market, developing effective pastureland management

techniques, and producing new varieties of herbage plants that could provide nutritious

grazings in poor soils and exposed upland conditions. R. George Stapledon, son of master

mariner and gun smuggler William Stapledon, took on all three of those problems. Prior to

the First World War, Stapledon helped establish what later became the first National Seeds

Testing Station (Moore-Colyer 1982, p. 90). His early research on grasslands focused largely

on the problem of converting crop-land back into rotational "ley" pasture, and reclaiming

Figure 1.3.1. Seed production at the Welsh Plant Breeding Station. Courtesy of the
National Library of Wales.

Figure 1.3.2. Field trials at the Welsh Plant Breeding Station. Courtesy of the National Library of Wales.

and restoring so-called "permanent" pastures: old pastureland that had become overgrown with perennial plants.

One of the formative insights of Stapledon's early research was that indigenous clovers, grasses, and herbage plants often outperformed commercial varieties in field trials. Around 1910, Stapledon assumed responsibility[17] for a long-term experiment modeled on the famous Park Grass experiments at Rothamsted Experiment Station. The project involved treating plots of permanent pasture-grasses with varying and cumulative applications of manure, to gain insights into the improvement of hay production. During the unusually arid summer of 1911, Stapledon noticed dramatic differences in mortality among

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[17] The project was initiated by Stapledon's mentor at the Royal Agricultural College of Cirencester, Edward Kinch.

the varieties of grasses in the experimental plots, especially in hard fescue (*Festuca duriuscula*): whereas sown commercial varieties suffered high mortality, the unsown indigenous varieties of the same species were far less dramatically affected (Stapledon 1913). Stapledon carried this idea with him to Aberystwyth in the autumn of 1912, when he was hired by C. Bryner Jones, Professor of Agriculture at UCW, to conduct a botanical survey of Mid Wales funded by the Board of Agriculture.

Stapledon's work on the botanical survey exposed him to what he considered an abysmal state of affairs in Welsh upland agriculture, and the improvement of hill grazings and farming practices quickly became a major plank of his research agenda. Together with Thomas James Jenkin, an Honours student in botany at UCW, Stapledon articulated a new vision for agricultural research and development in Britain. Inspired by the work of W. Gilchrist on wild white clover in the late 19th century, Stapledon and Jenkin argued that improvements in the long-term productivity of ley pasture could be best achieved by "making the habitat as suitable as possible to the desirable indigenous species"—thus altering the pattern of grassland succession to facilitate more productive and nutritious grazings—and by "establishing local supplies of ... indigenous seed" (Stapledon and Jenkin 1916, p. 62). In 1919, with help from former Food Production Department director Laurence Weaver, Stapledon successfully lobbied steel and shipping magnate Lord Milford to fund a new Welsh Plant Breeding Station. Stapledon, a graduate of the School of Agriculture at The University of Cambridge, sought to mirror the successful Institute of Agricultural Botany at Cambridge, and quickly enrolled substantial financial support from

the Ministry of Agriculture and the Empire Marketing Board[18] (Ellis 1972, p.199, Palladino 2002, p. 51).

The cornerstone of Stapledon's paradigm for plant breeding was sourcing material from local populations that had become adapted to prevailing conditions of soil, climate, and grazing. Prior to the establishment of the WPBS, in 1918 Stapledon undertook an ambitious survey of cocksfoot (*Dactylis* spp.) in Britain, continental Europe, and North America.[19] Stapledon took **advantage of the** resources and facilities of the new Station after its establishment in 1919 to conduct field trials of plants that he had collected abroad. He planted sampled material—often in the form of "tillers" (vegetative cuttings), if not seed—in spaced plots to assess the effect of agricultural conditions, such as simulated grazing, on the morphology and physiology of his various samples. High-performing samples became the basis for further selection and breeding programs aimed at producing new strains suited to the particular biotic and abiotic conditions of Welsh pastureland.

The agro-ecological methods that Stapledon employed belonged to a vein of research known variously among British botanists as *genecology* or *experimental taxonomy*.[20] The

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[18] Stapledon's proposal had erstwhile met resistance from the Development Commission.

[19] Sweden, Denmark, France, the United States, and New Zealand, as well as England, Scotland, and Wales.

[20] For an account of the origin and significance of the terms "genecology" and "experimental taxonomy," see Smocovitis (1988). The term "experimental taxonomy" was introduced by Harvey Monroe Hall and Frederic Clements at the Carnegie Institute of Washington in the 1920s and is associated with their successors, the "Carnegie trio," Jens Clausen, David Keck, and William Hiesey. The term "genecology" was introduced by Swedish ecologist Göte Turreson at about the same time. Historians have linked these terms to "biosystematics," introduced by W. H. Camp and C. L. Gilly in the 1940s. The common features of these approaches was the "common garden" methodology, and the integration of morphological, physiological, ecological, and cytogenetic data to address taxonomic,

core methodological theme of the genecological approach was raising plants sampled from a variety of different habitats in a controlled environment, or "common garden," facilitating the discovery and characterization of intraspecific varieties, or "ecotypes" (Turesson 1922b, Stapledon 1928, Smocovitis 1988, Hagen 1984). Stapledon considered the work of J. W. Gregor and F. W. Sansome on forage grasses near Edinburgh (Gregor and Sansome 1927), and of R. D. Williams (1927) on red clover,[21] to be exemplars of the genecological method in Britain (Stapledon 1928). Stapledon and Jenkin maintained a pattern of wide-ranging collection trips and experimental plantings, focusing on characteristics like growth rate, mortality, winter-hardiness, and disease resistance (Moore-Colyer 1982, p. 92). These field trials were often conducted in conjunction with cytogenetic research, which provided insight into which varieties could be hybridized to develop more desirable seed products. These efforts were galvanized by the post-war shift away from developing complex seed mixtures and toward producing individual high-performing varieties (e.g. Beddows 1949).

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ecological, and genetic questions about plants. Hagen (1984) and Smocovitis (1988) have largely emphasized the taxonomic dimensions of this interdisciplinary enterprise.

An examination of the bibliographies from Stapledon's and Gregor's writings in the 1920s suggest that they drew from Turesson's work at the outset. But in the 1930s through 1950s British ecologists appear to have used terms "genecology" and "experimental taxonomy" nearly interchangeably, with different degrees of emphasis placed on the taxonomic or on the ecological value of the approach. This began to change in the mid-1960s, when some ecologists began to more vocally and explicitly distance themselves from taxonomic concerns (see e.g. Valentine 1966, Bennett, 196x). Whereas Turesson based the term "genecology" on the Greek γένος ("race" or "stock"), British ecologists trained in the 1950s and 1960s often saw the term as synonymous with "genetical ecology." It could be hypothesized that this shift in thinking reflects increasing interest in questions about the interplay of gene flow, selection, and ecological processes in shaping plant populations. More research is needed.

[21] Williams' internationally recognized work on local varieties of red clover are described by Colyer (1982, p. 94).

Stapledon was increasingly vocal about the importance of converting "derelict" upland areas to productive ley farming, and of developing varieties that could remain productive in the harsher hilltop conditions for a greater portion of the year. This led to a privately funded[22] large-scale farm trial in the 1930s, the Cahn Hill Improvement Scheme, focused on grasses, clovers, and rapeseed (Moore-Colyer 1982, p. 101-104). This demonstration, combined with the rhetoric of war-time food security and the ecological data produced by William Davies' recent country-wide pastureland survey, commissioned by the Ministry of Agriculture in 1938, galvanized an argument for the 'ploughing-up' of British hill-sides.[23]

The genecological approach remained a dominant part of the research agenda at the WPBS when Bradshaw arrived in 1948. Bradshaw was greatly stimulated by Arthur Rhys Beddows, who had just returned from trip collecting ryegrass in the French countryside, Iorweth Jones, and other members of the Grass Breeding Department at the WPBS who perpetuated Stapledon's research program (D1041/13/2/9). Stapledon's vision for the reclamation of permanent pastures and upland areas for ley farming had not waned. In the 1948 edition of his book, Ley Farming, Stapledon insisted:

> We have squarely to face the fact that the food situation is as serious now as
>
> it was at any time during the war, and serious it will long remain. [...] The
>
> need of our country is for more milk [...], more meat, more vegetables, and

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[22] The Scheme was funded by Sir Julien Cahn, who had supported Stapledon's research at the WPBS starting in 1932. (Ellis 1972, p.238)

[23] Such rhetoric, combined with the outbreak of war in late 1939, prompted the Ministry of Agriculture to adopt Stapledon's recommendations for a Grassland Improvement Station on the 500-acre Drayton farm, south of Birmingham. Stapledon's directorship of the Drayton project, assisted by Davies, increasingly drew his attention away from the WPBS and, in 1942, Thomas James Jenkin took over as director of the Station.

always we must grow enough wheat and other cereals to supply a high

proportion of our own and our animals' needs. Ley farming is the system that

makes all this possible [...] wherever the plough can operate. [...] The ley

system can only win useful and food producing ground at the expense of

permanent grass. [...] *New knowledge on Grassland is accumulating fast, but there*

remains a great amount of detailed field work still to be done before the new evidence can be

used to the best practical advantage. (Stapledon, 1948. Preface.) [emphasis added]

Stapledon's forceful mandate was palpable. As Bradshaw himself recalled, during those early

years at Aberystwyth "the heritage of George Stapledon was never far away"

(D1041/13/2/9). There is no doubt that Bradshaw's nationalistic predilection for the

improvement of Britain would have made him all the more conscious of this fact.

Upon arriving at Aberystwyth, Bradshaw wasted little time in commencing his own

genecological research.[24] In early October, 1948, he began collecting brown bent[25] (*Agrostis*

tenuis Sibth., now *Agrostis capillaris*), sweet vernal grass (*Anthoxanthum odoratum*), and common

heath grass (*Sieglingia decumbens*, now *Danthonia decumbens*) from a variety of sites around

western Wales.[26] In the Stapledonian tradition, Bradshaw was on a hunt for ecotypes:

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24 The following account of Bradshaw's early research is drawn from a series of notebooks
that he kept over the course of his work, including methodological notes, general
observations, raw data, and sketches of his collection sites and both greenhouse and field-
trial layouts.
25 Also known as "Brown Top," "New Zealand Bent," and "Rhode Island Bent." Now
known more commonly as "Common Bentgrass," or "Colonial Bentgrass."
26 No notes regarding Sieglignia can be found in Bradshaw's surviving notes, but the
identity of that third species is substantiated by Askell Löve in a letter to Gregor, dated
September 13, 1949, based photographs from his visit to Aberystwyth several weeks prior.
(GD449/6/399) Bradshaw my also have worked briefly with Lolium, since his site at
Plynlimon is listed as an "experimental centre" for J. P. coopers transplant experiments
between 1947 and 1949. (GD449/6/105)

looking for populations of grasses that had become uniquely adapted to their particular

conditions of existence. The project would eventually include plants from more than thirty

sites, spread from the River Dovey to just south of the River Rheidol, and east to the

summit of Plynlymon at the northern end of the so-called "Green Desert" of Wales.[27]

Bradshaw sampled both on broad geographic scales, comparing lowland varieties to those

found atop the gentle peaks of the Cambrian Mountains, and on finer scales, comparing

plants on a given hillside to those found at its summit. He carried tillers from each site back

to Aberystwyth on a small motorbike, where he grew the plants in boxes for three months

before setting them out into experimental plots operated by the Grass Breeding Department

(D1041/13/2/9).

In the midst of these preparations, Bradshaw remained in contact with Gregor and

regularly sought his advice. In January, 1949, Bradshaw sent a progress report and a

summary of his research plans.

> Dear Dr Gregor, I have been meaning to write to you for some time, but Christmas
>
> rather got in the way, which only shows much one is attached to that Festival and
>
> festivity.
>
> I am now beginning to feel quite settled down in Aberystwyth. It has its
>
> advantages and its disadvantages, the main disadvantage being the remoteness from
>
> everywhere else. So I have been taking your advice and have been flitting round the
>
> countryside, for which purposes I have armed myself with a motorcycle.

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27 The highest summit of Plynlymon (Pumlumon) has an altitude of 2,468 ft, the highest
   peak in the Cambrian Mountains (also known as the Green Desert) of Mid Wales.

When I got down to work the main trouble that beset me was the enormous

lack of knowledge on the subject. Thus I found myself shedding one by one my

ideas of particular intensive observations in favour of a more general survey. It is for

this reason that I have chosen 3 species with which to work. But as a compromise

between general and particular I am trying to get a detailed picture of differentiation

within this area.

By this I feel I shall solve nothing but rather prepare the way for something

more detailed later on. All the time I find myself gaining techniques and ideas, and

becoming more attracted to the whole subject. (GD449/6/51–52)

Bradshaw asked Gregor for his advice on the structure of his project, and Gregor quickly

replied with encouragement and suggestions. Gregor suggested that Bradshaw focus on only

two species, rather than three, and to concentrate on three environmental gradients—

altitudinal, edaphic, and phyto-social—and to limit collection to the area around

Aberystwyth (GD449/6/53–54).

Bradshaw thus dropped *Sieglingia decumbens*, and focused more intently on *Agrostis

tenuis* and *Anthoxanthum odoratum*. Bradshaw's choice of organism was a reflection of the

research priorities of British genecologists working at both the Welsh and Scottish Plant

Breeding Stations. Interest in *Agrostis* among staff at Aberystwyth stemmed from a desire to

reclaim both acidic peaty soils and upland grazings for ley farming, which often involved

promoting the formation of *Agrostis-Trifolium repens* pastures (Stapledon 1948, ch. 11).

Toward that end, W. Ellis Davies, Keith Jones, and Alec Lazenby in the Grass Breeding

Department at the WPBS had begun developing strains of *A. tenuis* suitable for agricultural

use (Beddows 1958). *A. tenuis* and *A. stolonifera* were also popular as lawn grasses for sports

turf (Beddows 1958c), but despite commercial distribution little work had been done on the

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potential for controlled breeding (Jones 1956). Similarly, WPBS staffer Martin Borrill had

recently turned his attention to *Anthoxanthum odoratum* which, despite its relatively low yield,

was a promising candidate for developing acidic pastureland, and its rapid germination and

early emergence made it appealing for spring grazing (Meikle 1955, Beddows 1958).[28]

Agrostis is a ubiquitous feature of the British landscape. Stapledon described *Agrostis*

pastures as occupying "by far the largest aggregate acreage of any pasture type in Britain,

whether among the cultivated or the uncultivated pastures" (Stapledon 1948). William

Davies' country-wide pastureland survey, commissioned by the Ministry of Agriculture in

1938, indicated that *Agrostis* pastureland made up over 9.5 million acres in England and

Wales, representing over 60% of the total permanent grassland. While the *Agrostis* -dominant

pasturelands were generally found on more acidic soils, *Agrostis* could also be found in nearly

every other type of pasture assemblage, including upland hill grazings.

Along with *Agrostis'* ubiquity came a reputation for being taxonomically

incomprehensible. As the 19th-century British botanist John Leonard Knapp observed, the

genus *Agrostis* was a taxonomic mess:

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[28] John Leonard Knapp, 1842; Plate I:

> The first of our pasture grasses that peeps through the shades of winter, enticed by
> the sunny days of April, is this Anthoxanthum, and is immediately followed by the
> Meadow Foxtail. ... The early product of spring seems not much noticed by the
> grazier, and may not in its present situation claim peculiar attention, yet it seems
> unwise wholly to reject it: in pastures mixed with other grasses it is of little value,
> because by the time the scythe is introduced the Vernal-grass has faded, the foliage
> withered up, it being in perfection the first weeks in May, whereas grass is generally
> cut in June and July. Spring feed is our grand desideratum, and it may be questioned
> if this grass was selected and cultivated alone, as the Ray-grass is, if it would not
> prove in a certain degree valuable, by affording the most early food for lambs, as it
> flowers a full month earlier than the Ray-grass.

Figure 1.3.3. *Agrostis tenuis* and *Anthoxanthum odoratum*. From Knapp (1842).

There are none of the genera of our grasses which have been so little understood as the genus *Agrostis*, nor have we any race of plants that form more mutual concessions than this, melting down in the union all separate distinctions, at best but faint and weakly marked, and every soil at times shades to a variety: and such are the versatile habits of the species, that investigation, whatever the experience many be, seems at times confounded. From the acquirements of the earlier botanists we obtain nothing, as they gleaned the regions they passed through with a suspicious hand, and doubt hovering over all; they rejected none, but elevated into the rank of species the innumerable varieties of seasons, soils, and stations. Under these circumstances, we can expect to afford but little satisfaction in the

77

delineation of individuals so very capricious as this is; [...] but those who have looked deeper are aware of the delusory character of *Agrostis*, and the difficulties to contend with. (Knapp 1842).

After planting his samples of *Agrostis* and *Anthoxanthum* in the Grass Breeding Department plots, Bradshaw monitored their growth closely, vigilant for signs of physiological or morphological differences between the populations. In addition to studying their growth habit (e.g. their tendency toward stoloniferous or rhizomatous growth) and overall morphology, he kept detailed notes on their susceptibility to winter burning and the timing of emergence of new tillers. In April, 1949 he noted flowering time, and collected pollen samples from varieties of both *Agrostis* and *Anthoxanthum* for cytologist Keith Jones, who was eager to characterize what were, from the cytological perspective, two very understudied grasses (Jones 1956).

In the summer of 1949, with the help of WPBS staff in the plant breeding department, Bradshaw established five experimental plots in a set of contrasting environments in western Wales, into which he transplanted tillers from some of the populations of *Agrostis* that he had sampled. There is little doubt that the work of the "Carnegie trio," Jens Clausen, David Keck, and William Heisey of the Carnegie Institution of Washington in California (described on pages 71–72) was enormously influential for Bradshaw.

In Bradshaw's reciprocal transplant experiments, the range of altitudes was diminutive in comparison to the Carnegie project, ranging from coastal plots near the shores of Cardigan Bay and the Dovey estuary (20 feet above sea level), to the top of Pen Plynlimon

Arwystli (2,400 feet). His sites varied somewhat more dramatically in average rainfall, ranging

from 20 inches per year at Hen Hafod, on the the southeast side of the Dovey estuary, to

100 inches at Plynlimon (Bradshaw 1960). Bradshaw established two plots at Hen Hafod:

one on silty estuarine clay, often waterlogged in wetter periods due to poor drainage, and

another on a deeply acidic bog peat nearby (D1041/3/36/5). Another plot was situated in an

oak wood at Nanteos, a few miles east of Aberystwyth.

In addition to considering the influence of climate and soil acidity on ecotypic

differentiation in *Agrostis* and *Anthoxanthum*, Bradshaw also turned his attention to the toxic

tailings of a disused lead mine, a common blight on the Welsh countryside. The spoil heaps

at the old Goginan Mine in particular, six miles up the river Rheidol from Aberystwyth, had

commanded the attentions and anxieties of botanists and zoologists at the University College

since the 1920s. Zinc and lead sulphates in the waste heaps (formed by oxidation of latent

sulphides during dry weather) were easily dissolved in rainwater, which flushed the toxic

metal into the river and estuary downstream with disastrous biological effects (Jones 1940).

Plant growth on the spoil heap itself was virtually non-existent, and those few plants that

were found on it were sickly and prone to fungal infection (Newton 1944). Lily Newton,

Professor of Botany at Aberystwyth in the 1930s,[29] had long studied the effects of the toxic

soil on plants and aquatic organisms. Newton and her colleagues hypothesized that the

paucity of plants on the mine tip was caused by a deficiency in phosphates, which were used

up in chemical reactions with zinc (Newton 1944). The toxic soil itself was continually

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[29] Newton was well-known for her work on marine algae .Newton was the widow of
cytologist William Charles Frank Newton, hired by William Bateson at John Innes in the
1920s. William Newton trained C. D. Darlington in cytology between 1924 and 1926,
before an early death at the age of thirty in 1927. Lily Newton moved to Aberystwyth in
1928, and was promoted to Professor in 1930.

redistributed by winds, such that "in the case of young pine trees [the accumulation of toxic material] kept pace with the annual growth so that only the uppermost whorl of branches was ever exposed" (Newton 1944, p. 8). By the mid-1940s, Newton thought that the only real hope for preventing further erosion of the heap was to cover the toxic soil with a binding substance like bitumen, or to overlay the heap with soils more favorable to plant growth.

On 30 October, 1949, having read Newton's book, *Plant Distribution in the Aberystwyth District* (D1041/3/13), Bradshaw visited the mine at Goginan (D1041/2/9/36). Among the few plants growing on the mine tip, Bradshaw found a sickly assemblage of *Agrostis*.

> The [plants] on the mine waste were miserable things and I thought that
> selection might have made them different in some way. Then going back to
> my old interest in soil, I managed to persuade the A.R.C. to finance a series
> of plots on different soils. To set these up properly I decided not just to plant
> the material directly into the plots, but to start them off from the beginning
> in boxes on different soils which I carefully hauled back to Aberystwyth. So
> the Goginan pair were planted out in the autumn [of 1949] on normal and
> mine soil. (D1041/13/2/9)

Bradshaw set the Goginan pair aside by a hedge for the winter, planning to return in spring to transplant them into experimental plots.

Meanwhile, not everything went smoothly for Bradshaw in the early stages of his research. That summer, morphological differences among his collections of grasses were muted, especially among the *Anthoxanthum* populations. By September the *Anthoxanthum* (which tended to prefer wetter conditions) had suffered catastrophic mortality at the hands

of severe drought. Worse, when he returned to the oak wood at Nanteos in November, the ink of his Biro blue pen had almost entirely faded from the paper labels that he had used to track the identities of the various samples in his experimental plots (D1041/2/7/3). Henceforth, Bradshaw's research notebooks featured plot diagrams with the precise layout of the various samples.

Little did Bradshaw know that, mid-stride in his graduate research, his life was about to become even more complicated. That winter Bradshaw was offered an unexpected position as Lecturer in the Department of Agricultural Botany at the University College of North Wales in Bangor. The move, although welcome, would delay the completion of his dissertation by about seven years. But it would also open new directions that would shape the trajectory of his career.

CHAPTER 2: MICROEVOLUTION ON MICROSCALES

In 1950, Bradshaw moved to Bangor, in northwestern Wales. Between 1950 and 1968 he developed a multi-pronged research program concerning local adaptation in a variety of plant species. Bradshaw's research amplified and transformed the Gregorian-Stapledonian genecological research program.

2.1. The Move to Bangor

Bangor is a small city on the banks of the Menai Strait, a roughly sixteen-mile channel separating the island of Anglesey from the mainland of northwestern Wales. The city itself is nestled between two high ridges—Bangor Mountain to the southeast, and Upper Bangor to the northwest—opening to eastern views of the Irish Sea. The incoming tide sweeps through the Menai Strait twice per day, creating a spiderweb of treacherous currents in the shoal-riddled bay at its northeast opening (known as the "swellies") before pushing up the river Mersey to Liverpool. The establishment of a ferry in the early 18th century at Porthaethwy, a bend in the strait to the immediate southwest of the city, followed by the construction of a suspension bridge on the same site in the 1820s, placed Bangor on the main route between London and Dublin via the Port of Hollyhead on Anglesey. The arrival of the railway two decades later would solidify Bangor's position as the foremost economic center in north Wales. Bangor would also become a major center for higher education, home to Bangor Normal College, the University College of North Wales, and St. Mary's College by the end of the 19th century.[30]

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[30] St. Mary's College was incorporated into UCNW Bangor in September, 1977. (Roberts, p.84); Coleg Normal followed suit in 1994 (Roberts, p.114). The University of Wales was defederated in 2007, and UCNW Bangor was renamed Bangor University. (p.122)

Figure 2.1.1. University College of North Wales, Bangor, in the 1950s. Casgliad Geoff Charles Collection. Courtesy of the National Library of Wales.

The University College of North Wales, Bangor, was one of three founding colleges in the federal University of Wales.[31] The University College of Wales in Aberystwyth emerged from fitful beginnings in the 1870s, and in 1883 Bangor and Cardiff were chosen as the sites of two new colleges to serve northern and southern Wales, respectively (Roberts 2009). Of the three, Bangor was the first to establish a school of Agriculture (Ellis 1972, p.105),[32] UCNW quickly became known as "the agricultural headquarters of north Wales," (Roberts 2009, p. 24.) "set[ting] the fashion for the whole kingdom" (Manchester Guardian 1899) in matters of agricultural education. After a period of economic depression and

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[31] The University of Wales was defederated in 19

[32] The first Professor of Agriculture at Bangor was appointed in 1895: Thomas Winter, Professor of Agriculture (1895-1913) (Roberts 2009, p. 24).

Figure 2.1.2. The Memorial Building at UCNW Bangor. Home of the School of Agriculture. Bangor Civic Society. Retrieved from bangorcivicsociety.org.uk.

declining enrollment in agricultural programs during the late 1920s and 1930s, following the Second World War the College established a new Professorship in Agricultural Botany within the School of Agriculture. The foremost emphasis of the Department of Agricultural Botany was training plant breeders. As contributions to British society went, service in agricultural professions was ranked second only to military service in the rhetoric of wartime Britain. Thus by the late 1940s there were two botanical units at Bangor: the long-standing Department of Botany, chaired by David Thoday (1883-1964), and the Department of Agricultural Botany led by R. Alun Roberts, who had served as the Ministry of Agriculture's Grassland Advisor for Wales during the war (Roberts 2009, p. 38).

Figure 2.1.3. Staff in the Department of Agricultural Botany at Bangor, early 1950s. From left to right: Bradshaw, Dafydd Wyn Parry (lecturer), Margaret Mence (assistant lecturer, plant diseases), Professor R. Alun Roberts, unknown female, Frank (lab tech), unknown female. Courtesy of the University of Liverpool Sydney Jones Library Special Collections & Archives.

Shortly after Bradshaw arrived at Aberystwyth in 1948, Cambridge ecologist Paul W.

Richards was tapped to replace Thoday as chair of the Department of Botany at Bangor.[33]

Richards arrived at a moment of rapid growth in undergraduate enrollment. In 1949 the

Botany department reported a new cohort of students numbering "three times the average

of pre-war years" (UCNW Reports of Department Heads, 1947-1948). Indeed, the entire

college was bursting with undergraduates, growing from 380 students in 1944 to over 900 by

1947 (Roberts 2009, page 64), driven predominantly by an influx of ex-servicemen. This

rapid expansion left many academic departments scrambling for teaching staff. Upon

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[33] Thoday had served as Chair of Botany since 1926, following a period as Professor of Botany at the University of Cape Town from 1918. (Stiles 1965).

Richards' arrival in 1949 the two botany departments began to collaborate closely in both teaching and research: faculty members from each department shared laboratory equipment, and frequently provided lectures for their counterparts' students (UCNW Reports of Department Heads, 1949-1950).

The heightened demand for teaching staff at Bangor created an unexpected opportunity for Bradshaw. Ecologist R. Elfyn Hughes (discussed below) left Bangor for a Lectureship in the School of Agriculture at Cambridge in 1949, increasing the strain on an already thinly spread teaching staff in the Department of Agricultural Botany. That June, Roberts began circulating the job posting for a Lecturer to replace Hughes. In a form letter sent along with the posting, Roberts wrote that, "Dr. Hughes is a specialist in ecology and I would like to replace him with a worker in the same field, as a first choice, but applications from general agricultural botanists will be equally welcome" (GD449/6/503).
Yet no suitable candidates had emerged by the July 30 application deadline (GD449/6/504). The difficulty of finding suitable candidates prompted Roberts to expand his search, making someone like Bradshaw—who was only midway through his Ph.D. research—a potential fit. Paul Richards had been impressed by Bradshaw's lectures as an Exhibitioner at Cambridge, and later that year invited him to interview for the Lecturer position.

When Richards called Bradshaw about the Lecturer post, Bradshaw saw it as a welcome reprieve from the boring "slog of doing research" and "the difficulty of having new ideas for it" (D1041/13/2/9). So Bradshaw made the three-hour journey north to Bangor, where he was asked to take responsibility for courses in evolution, plant breeding, and grassland ecology. Ironically, though perhaps an indication of the extent to which Bangor lacked a strong cytogenetic research program, Roberts enthusiastically hailed Bradshaw's

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coming as having "greatly strengthened the Department in the field of cytogenetics"

(UCNW Reports of Department Heads, 1949-1950).

Bradshaw took well to his new responsibilities,[34] which found him lecturing to

students in the Departments of Botany, Forestry, and Agriculture. Bradshaw was expected to

teach "in the whole field of Agricultural Botany (to Honours standard), with the exception

of Plant Pathology" (GD449/6/505). Close collaboration between the Botany and

Agricultural Botany programs meant that Bradshaw's pedagogical remit extended to both

future plant breeders and more traditional botany students. Bradshaw also immersed himself

in student culture and community life at Bangor. The job was all that he could wish for

(D1041/13/2/0).35

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[34] In developing his lectures, Bradshaw built on some of his own coursework at Cambridge: he kept well-organized folders of notes on each topic under his remit, supplementing his own lecture notes with bibliographies and corresponding annotations of both historical and contemporary literature, which he updated every few years. The residues of Bradshaw's training under Harry Godwin at Cambridge were evident in his lecture notes on quaternary science and pollen analysis.

35He served as a tutor in Neuadd Reichel (one of the college residence halls), where he oversaw the design and care of the surrounding gardens. In his spare time he often took to the water, coaching the top two boats in the college rowing club. He helped to develop a new boathouse in Nant Porth at the eastern opening of the Menai Strait, and founded the college sailing club, which became one of the most popular sports clubs in Bangor. He also continued to nurture his passion for the arts as an active member of both the English Dramatic and Gilbert and Sullivan Societies. serving as scenery designer, assistant stage manager, and doing a bit of performing himself.
    1-4 December, 1954: Patience by W. S. Gilert & Arthur Sullivan (Gilbert & Sullivan Society). Chorus of Dragon Guards.
    28-29 January, 1955: Ring Round the Moon by Jean Anouilth (English Dramatic Society). Scenery Design.
    29-30 November, 1957: The Pirates of Penzance by W. S. Gilbert & Arthur Sullivan (Gilbert & Sullivan Society). Assistant Stage Manager. Bradshaw would later become one of three trustees of the student body's Cultural and Development fund. D1041/13/3/45/2

The move to Bangor and the Department of Agricultural Botany also meant immersion in an intellectual culture in which the boundaries between ecological research and ecosystem management were blurred. "By modern standards it was a very small department (5 staff)," Bradshaw wrote, "There were usually 5-10 honours students only, but they were a very lively bunch who we got to know well as a result of much time spent on field trips under the guidance of our fascinating Professor, Alun Roberts, who had a remarkable understanding of Welsh agriculture, history, and grassland ecology. [...] I learnt a great deal of ecology—very different from what I had been given in Cambridge. It was very holistic— about ecosystems and how to manage them for human needs" (D1041/13/2/9).

The idea that ecology and management were inextricably linked resonated with Bradshaw. Bradshaw's own course materials featured notes on the relationships between human agricultural activity and the ecology of Britain, and the interpenetration of scientific research and problems in plant breeding, agriculture, and natural resource management. Echoes of this holistic and integrative view can be heard in Bradshaw's call for a scientific approach to ecological restoration in the early 1980s: Bradshaw thought that the ability to apply scientific knowledge to change an ecosystem to meet human needs was the "acid test" of ecology. Both Bradshaw and John Harper, who would assume Professorship of the Department in 1960, envisioned a reciprocal and interdependent relationship between restoration efforts and ecological research.

Figure 2.1.4. Bradshaw assisting the Felinheli Sailing Club with an exhibition of sea rescue techniques. May 19, 1960. Courtest of the National Library of Wales. Casgliad Geoff Charles Collection. (WlAbNL)003366279

Bradshaw's teaching responsibilities at Bangor made for slow progress on his dissertation research, but he did what he could to move it forward. In early March of 1950, he followed up on the catastrophic drought-induced mortality in his *Anthoxanthum* samples. Perhaps inspired by Stapledon's report of drought-tolerant ecotypes in 1911, Bradshaw scrutinized his data for differences in mortality between the populations. Indeed, those collected from the driest locales, such as a rocky outcrop along the coast, had a much greater resistance to the drought conditions than those collected from the bogs (D1041/2/8/1). Hoping to bring some quantitative data to bear on the situation, he wrote to a hydroelectric engineer at the British Electricity Authority to request rainfall figures for his field sites

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(D1041/2/8/19-21). The correlation between average rainfall at each site and the mortality of grasses that had originated there was striking. Bradshaw returned to the field in April to collect more of the *Anthoxanthum*, storing the samples in an unheated greenhouse at Aberystwyth until he could plant them out again in the summer (D1041/2/8/6/1-2).

In the meantime, Bradshaw had returned to his *Agrostis* samples from the Goginan mine that spring to make a startling—but ultimately fortuitous—discovery. Here, too, he found that many of the plants had died off, but this time for a very different reason. "[W]hen I came to look at [the *Agrostis* from Goginan] mine," Bradshaw wrote, "there seemed to be a disaster—about half the plants were dead—and I castigated myself for being so sloppy and not caring for them properly. But about two days later I thought I better look at them again. Lo and behold what had happened was that on the mine soil it was just the pasture plants that had died. I could not believe it—but it was true—I spent a very exciting afternoon measuring and taking photographs" (D1041/13/2/9).

Figure 2.1.5. Differences in root growth between tolerant (right) and intolerant (left) varieties of Agrostis growing at Goginan lead mine. Bradshaw wrote that the Goginan soil "ties roots up in knots." Photo: D1041/2/9/37/1. Quote: D1041/2/9/36. Courtesy of the University of Liverpool Sydney Jones Library Special Collections & Archives.

Bradshaw's measurements of the Goginan *Agrostis* from that afternoon in the summer of 1949 are summarized in figure 2.1.6. The previous autumn, Bradshaw had planted 58 tillers from plants found growing on top of the Goninan mine tip (G1), and 59 tillers from plants found growing in the nearby pasture (G2). Whereas 55 of the G1 tillers rooted successfully, only 37 of the G2 tillers formed roots. Moreover, the G1 plants had considerably more root mass and formed a greater number of tillers.

Bradshaw's discovery of the metal-tolerant plants at Goginan would later become the nucleus of his work on both microgeographic differentiation in plant populations, as well as his contributions to restoration ecology. A few months later, at the 7th International

Botanical Congress in Stockholm, Sweden, the "Goginan pair" was forefront in Bradshaw's

mind. At the Congress, Bradshaw injected his preliminary findings into a lingering

conceptual and epistemic tension over the nature and diagnosis of ecotypic differentiation.

2.2. The Speed, Scale, and Specificity of Natural Selection

The 7th International Botanical Congress, held in Stockholm, Sweden, in July of 1950, was

Bradshaw's first ingress into an international scientific arena. Along with many other

attendees from around the world, he arrived early to take advantage of the many excursions

organized as part of the Congress.[36] Late in the trip, Bradshaw visited the Institute for Plant

Systematics and Genetics at the Royal Agricultural College of Sweden in Uppsala, where

Göte Turesson gave Bradshaw a tour of his botanic gardens. During the visit, Turesson

discussed regional variation in germination in a variety of Swedish plants (D1041/3/12), and

pointed out two varieties of water knotweed (*Polygonum amphibium*)—known for its ability to

adopt alternate growth forms corresponding to terrestrial and aquatic conditions—one of

which seemed to lack the morphological plasticity characteristic of the species

(D1041/4/3/20). Those plants would play an important role in Bradshaw's thinking about

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[36] On July 6, Bradshaw attended an opening reception at the Akademiska Föreningen, Lund. Over the the next four days, Bradshaw took bus trips to a variety of agricultural research centers around southwestern Sweden. These included the Horticultultural Research Station at Alnarp, the Institute of Genetics and Botanical Garden at Lund, the Svalöf Plant Breeding Institute and Swedish Seed Association, the Svalöf branch of the Institute of Genetics, the Weibullsholm Plant Breeding Institute in Landskrona, the Sugar Beet Breeding Institute at Hilleshög, and the Institute of Forest Tree Breeding at Källstorp.

adaptive phenotypic plasticity, a decade later.
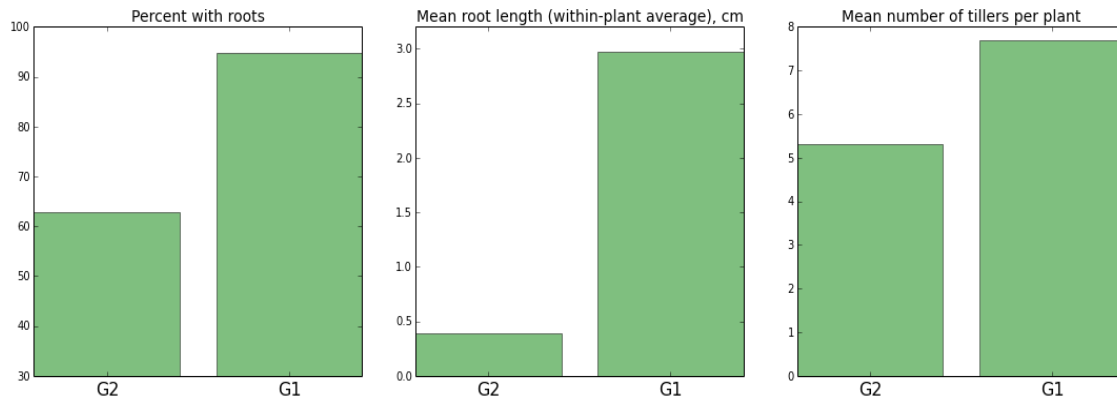
Figure 2.1.6. Summary of Bradshaw's measurements (summer, 1949) of *Agrostis tenuis* sampled from the Goginan mine tip (G1) and a pasture nearby (G2), growing in an experimental plot on contaminated soil from the Goginan mine. Root length was first averaged within each plant, and then across all plants in the population sample (including non-rooting plants). Calculations by Bradshaw. Transcribed from Bradshaw's notebook, D1041/2/9/36.

The Stockholm Congress brought to the foreground certain themes that remained central to Bradshaw's investigative trajectory throughout the 1950s. In an afternoon session (titled "Wild populations, discontinuity, and the ecotype concept") on July 17, 1950, Frederick Earnshaw gave a short presentation laying out the present state of debate concerning the methods of genecology. Earnshaw, a staffer at the SPBS (Anonymous 1952), had worked with Gregor, Erna Bennett, and others on an extensive study of *Plantago maritima* in North America and Europe (e.g., Gregor 1939, Earnshaw 1942). According to Earnshaw, the ecotypes of *Potentilla glaundulosa* described by Clausen, Keck, and Hiesey were more fittingly ranked as sub-species (Keck, present in the audience, objected to this claim), suggesting that the Carnegie group assumed that the major boundaries of ecotypic differentiation were policed by long periods of reproductive isolation. In contrast, Earnshaw observed, Gregor advocated a move away from attempts to diagnose distinct ecotypes, and

toward tracing patterns of hereditable variation in particular characters ("ecoclines") in relation to environmental gradients on local scales (Osvald and Abert 1954). Moreover, Gregor thought that such differentiation could occur on scales even smaller than the probable distance over which a plant could disperse its genetic material.[37]

Earnshaw's presentation raised two epistemic problems. Earnshaw's suggestion, following Gregor, that the term "ecocline" be reserved for cases in which a character had been shaped by selective pressures generated by a specific ecological gradient was met with some consternation from David Webb of Trinity College, Dublin. Webb questioned whether, given the complexity of most ecological situations, one could ever obtain sufficient evidence to make claims about the adaptive relationship between any one character and any one environmental parameter. David Keck expressed skepticism that meaningful ecotypic differentiation could be diagnosed in the first place on the basis of a single character, reflecting the Carnegie group's conception of ecotypes as relatively stable groups distinguished by *sets* of characters suiting those plants to more disparate environmental circumstances (Osvald and Aberg 1954, pp. 270–271, Hagen 1982, p. 90).

Bradshaw interjected that both of the problems posed by Webb and Keck could be settled through "extensive cultivation experiments of the plant in habitat from which they originally came." Pointing to his fortuitous discovery of lead-tolerant *Agrostis* only a few months prior, Bradshaw asserted that such experiments could reveal differences in survival, and that the small scale over which some differentiated populations were distributed—"an area ... only 70 yds. across"—made a strong argument for further scrutiny of local

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[37] Russian genecologist Evgenija Nikolaevna Sinskaja had proposed a two-tiered system, with major climatic ecotypes—perhaps comparable to those of the Carnegie group—divisible into smaller "ecoelements" adapted to local ecological situations.

differentiation. Thus by 1950 Bradshaw was already convinced that natural selection could act to differentiate adjacent populations on very small spatial scales.

Upon returning from Stockholm, Bradshaw set to work on *Agrostis* with renewed vigor. Perhaps due to wetter weather and muted results in his drought-tests with *Anthoxanthum*, Bradshaw seems to have set that project aside.[38] In August and September of 1950 he spent long days in the *Agrostis* plots at Aberystwyth, recording the extent of flowering in each population sample. With the help of Ellis Davies, whose interest in the potential of breeding new varieties of *Agrostis* for pasture improvement had grown, Bradshaw also spent time disentangling a case of rampant hybridization between populations of *A. tenuis* and *A. stolonifera* that he had encountered at Port Meadow near Oxford, using methods modeled on his undergraduate study of *Crataegus*.[39] Over the next three years Bradshaw would continue to monitor his experimental plots at Aberystwyth and his five field sites, with differences between the populations becoming more pronounced from year to year.

And then there was the "Goginan pair" of *A. tenuis* populations. Prior to Stockholm, on 30 October 1949, Bradshaw had returned to Goginan and sampled tillers of another sixty plants from each population—those growing on the mine tip (G1), and those growing in the adjacent pasture—and planted the tillers in uncontaminated soil. One year later, Bradshaw sought to replicate the results of his fortuitous experiment the previous winter. This time, Bradshaw collected soil from both the Goginan mine tip as well as from the Frongoch lead

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[38] Bradshaw does not appear to have recorded the results of his drought-resistance tests in the summer of 1950, so it is not entirely clear what became of that effort. He resumed work on *Anthoxanthum* by November, 1951, when he started a series of frost resistance trials with plants from three of his field sites. D1041/2/8/13.

[39] [some notes on method—metrical versus discrete characters?]

and zinc mine, about 15 km ESE of Aberystwyth. On 26 October 1950, he transplanted

tillers from the G1 and G2 populations onto both the Goginan and Frongoch soil: one or

two tillers per pot, three replicates per soil type (D1041/2/9/36).

The choice to use soil from two different mines appears to be Bradshaw's first

attempt to address the specificity of the Goginan *Agrostis*' apparent adaptation to

contaminated soils. The problem of the specificity of ecotypic adaptations in relation to

environmental factors, posed by Webb at the Stockholm Congress, would become one of

the dominant planks of Bradshaw's research agenda in the second half of the 1950s.

About six months later, on 27 March 1951, Bradshaw returned to Aberystwyth to see

how the Goginan plants had fared. Once again, individuals collected from the mine tip were

able to grow on the mine soil, while those from uncontaminated pasture nearby could not.

And once again, the difference seemed to lie in the roots: the contaminated soil (especially

the soil from Goginan) seemed to "tie roots up in knots" (D1041/2/9/36). Bradshaw

reported his findings in a letter to the journal *Nature* in 1952. Gregor wrote to Bradshaw to

express his approval, hailing the discovery as "an excellent example of how localized

ecological differentiation can be" (D1041/2/9/7).

The implications of Bradshaw's findings for land reclamation were obvious, and his

letter to *Nature* about the heavy-metal tolerant *Agrostis* at Goginan aroused interest beyond

the field of genecology. Within a few months of the June, 1952 announcement Bradshaw

began to receive a steady stream of inquiries about the potential use of his grasses to stabilize

polluted soils, foreshadowing his work in restoration ecology some decades later. The first

letter came from the Agricultural Chemist J. W. McGarity at the University of Sydney,

Australia, who hoped that Bradshaw's *Agrostis* might help to stabilize contaminated soils

being spread by flooding and wind in the mining district of New South Wales

(D1041/2/9/10/1). While Bradshaw had only just begun to sort out what it was, precisely, that allowed his unusual plants to grow on contaminated mine tailings, he was very eager to help.[40] Over the next few years Bradshaw would continue to receive similar requests from organizations such as the Nature Conservancy (D1041/2/9/14/1) and the Local Government Board of the Isle of Man (D1041/2/14/36/3, D1041/2/14/36/8).

Although Bradshaw's investigation was from the outset a search for ecotypic differentiation in populations of *Agrostis*, he did not hide the fact that he was unprepared to address the physiological mechanisms of the differences in heavy metal tolerance that he had found. So Bradshaw solicited input from Herbert Baker at the University of Leeds (D1041/2/9/2), who suggested that he contact Arthur R. Kruckeberg at the University of Washington.[41] In the early 1940s Kruckeberg worked as an assistant to the Carnegie group on their transplant experiments in coastal California, and in 1950, submitted a dissertation to the University of California at Berkeley[42] concerning intraspecific differentiation in plants growing on magnesium-rich serpentine soils (Kruckeberg 1951). In a reply to Bradshaw dated August 2, 1951, Kruckeberg confirmed that he had found many plant populations uniquely adapted to the serpentine soils, but noted that in most cases the plants were not actually adapted to the magnesium itself, but rather to associated deficiencies in basic nutrients such as nitrogen, potassium, and phosphate. He suggested that, similarly, Bradshaw's *Agrostis* might be adapted to scarcity of certain nutrients precipitated by lead and zinc in the mine-tip soil (D1041/2/9/1).

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[40] After a brief tussle between McGarity and the Commonwealth Chief Quarantine officer over import policies, Bradshaw shipped a box of tillers to Sydney.

[41] In the beautiful city of Seattle, Washington.

[42] Kruckeberg's dissertation was supervised by Herbert Mason, Hans Jenny, and G. Ledyard Stebbins (Olmstead, 2007).

Bradshaw was already familiar with Lily Newton's hypothesis that phosphate deficiency in the Goginan soil explained the general paucity of plant growth. Bradshaw replied to Kruckeberg, "I think you are probably quite right about the effect of lead and zinc being one of removing essential elements, rather than being due to direct toxicity ... the population from the lead mine may well owe its survival to tolerance of low concentrations of phosphate" (D1041/2/9/61). In December, 1952, Bradshaw wrote to Hans Hahn at the Max Planck Institute for Bast Fiber Research that, "the discovery … of resistant populations of Agrostis tenuis was made quite by accident ... so I don't know as yet very much about this character of resistance. I want to find out whether it is in relation to lead, zinc,[43] phosphate deficiency, excess sulfate or some other factor" (Letter from A. D. Bradshaw to H. Hahn; December 19, 1952).

On the same day, Bradshaw offered a tentative hypothesis and a plan of action to Roger Lambion at the National Institute of Industrial Fermentation, in Brussels. "At the moment I rather think that zinc is the most important since its compounds are the most soluble. ... I am going to try now various methods such as those mentioned in the paper by C[lark] M[aurice] Keaton, 1937. When I have some idea of which is the best method, I will write to you again and also give you some of my findings" (Letter from A. D. Bradshaw to R. Lambion; December 19, 1952).

The method to which Bradshaw referred in his letter to Lambion was a soil-culture technique that Clark Maurice Keaton,[44] soil chemist at the State College of Washington's

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[43] Zinc is commonly found alongside lead at contaminated mine sites like Goginan.

[44] Chemist Clark Maurice Keaton received his Ph.D. in 1938 from the State College of Washington (now Washington State University), where he worked as an instructor in soils in the College of Agriculture and Experiment Station.

Agriculture and Experiment Station, had developed in the 1930s to isolate the effects of a single dissolved mineral—in this case, lead—on the growth of barley plants. Keaton collected, dried, and potted uncontaminated soil from an orchard, into which he poured aqueous solutions made from varying concentrations of lead salts. By extracting the lead that built up in the roots and tops of the barley plants grown in that treated soil, Keaton was able to assess the relationship between soil concentration, uptake, and its effects on growth.

Bradshaw envisioned modulating a whole array of minerals and nutrients using methods similar to Keaton's. Such an experiment could provide evidence that the distribution of tolerance that Bradshaw found at Goginan was specific to the distribution of a particular chemical feature of the soil. This would not only address Newton's phosphate-deficiency hypothesis, but also go some way toward addressing Webb's concerns about attributing the distinct features of ecotypes to selective forces precipitated by specific environmental factors.

In his correspondence with Kruckeberg in late 1951, Bradshaw outlined two additional, intertwined lines of investigation. "I intend as far as this tolerance for lead contamination in *Agrostis tenuis* goes," he wrote, "to investigate the populations of lead mines of different ages and different degrees of isolation from other [populations], to see what part these two factors may play in the development of tolerance" (D1041/2/9/61) In his first letter to Kruckeberg, he had noted that "there are mines of different known ages of from 2,000 to 70 years, which suggests possible interesting lines of work" (D1041/2/9/62).

The first such "interesting line of work," foreshadowed at the Stockholm Congress in 1950, was to seek a better understanding of the interplay of gene flow and natural selection in shaping patterns of differentiation. Gregor's suggestion that "a spatial separation well within the dispersal limits of pollen is apparently sufficient to afford a degree of

isolation which will allow communities to assume a genetic individuality of their own" (Gregor 1946, p. 256), implied that such differences were actively maintained by powerful natural selection. Disentangling the problem of ecotypic differentiation, therefore, required a more detailed understanding of the dynamics of dispersal, differences in mortality, and the availability of standing genetic variation on which selection might act. Bradshaw confided to Kruckeberg in 1952 that it was questions of "population genetics or genetical ecology" that interested him most (D1041/2/9/61).

The second line of inquiry that Bradshaw proposed in his letter to Kruckeberg is summarized by a simple question, scrawled in his greenhouse notebook in April of 1952: "Length of time for differentiation?" As Bradshaw had explained to Kruckeberg, "Before excavation, the soils over the lead rich veins are completely normal. This is well born out by the original prospectors who had great difficulty in locating them. So one can assume that the specific environment of lead contaminated soil dates from the opening of the mine" (D1041/2/9/61). The age of a mine, then, would provide a probable upper bound on the duration over which mine-tip populations had diverged from their non-tolerant neighbors.

The first step in Bradshaw's "plan of campaign" was to compare resistance in the Goginan pair to lead- and zinc-contaminated soils, starting with soil collected from the mine tips at Goginan, Frongoch, and Trecastell. They would also analyze the metal content of soil from each site, in the hope of pinning down more specifically the substances to which the plants were resistant (D1041/2/9/56). Bradshaw intended to carry out further surveys at sixteen different mines around Wales (D1041/2/9/57).

Although the problem of quantifying gene flow and selection would remain an open area of research for Bradshaw into the late 1960s, by 1953 Bradshaw had already made up his mind about the efficacy of natural selection to effect differences between populations on

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small spatial scales. Citing the recent findings of breeders at the WPBS that pollen dispersal in even wind-pollinated grasses could attenuate dramatically over a distance of 100 feet, in an April, 1953 paper to the Genetical Society of Great Britain he insisted that such gene flow "would easily be overcome by natural selection" (Bradshaw 1953). He later wrote that, "It seemed to me self evident that natural selection could be strong enough to differentiate populations and overcome any exchange of genes tending to overcome this. And lots of my populations showed this" (D1041/13/2/9).

Bradshaw's ideas about the power of selection to induce microgeographic differentiation met resistance from the Carnegie group. In the summer of 1953 the monumental task of recording and analyzing the differences in the more than thirty *Agrostis* populations had drawn to a close. On a visit to the WPBS, Keck dismissed the differences that Bradshaw had found between closely adjacent *Agrostis* populations as "accidents" (D1041/13/2/9). Such a dismissal was incredibly discouraging for Bradshaw, who deeply admired the work of Keck and his colleagues at the Carnegie Institute.

Yet with the encouragement of Gregor and Pat Watson at the SPBS, "Fritz" Ehrendorfer in Vienna,[45] and the WPBS staff, Bradshaw took his ideas about microgeographic differentiation before an international jury. In late August of 1953 Bradshaw traveled to the peninsular *comune* of Bellagio on Lake Como, in northern Italy, where he presented his work on *Agrostis* at the 9th International Congress of Genetics. Bradshaw repeated his assertion that "local population differences are to be expected whenever natural selection is sufficient to overcome gene flow," which he considered, "likely to occur commonly in plants" (Bradshaw 1954). Bradshaw's paper was well received, an

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[45] Likely an acquaintance from the Stockholm Congress in 1950.

enormous encouragement to the young ecologist. Among the members of Bradshaw's audience in Bellagio was population geneticist Theodosius Dobzhansky who, on a boat trip on Lake Lugano later in the conference, strongly encouraged Bradshaw to continue his investigations.

Despite the encouraging reception of Bradshaw's work at Bellagio, and his own best intentions, progress on the lead-tolerant *Agrostis* was slow. In an October 1, 1954 letter to Werner Krause at the National Research and Advisory Institute for Agriculture in Baden, Germany, Bradshaw wrote,

> I have not yet been able to do any more work with this population of
>
> Agrostis tenuis resistant to lead and zinc poisoning but I am hoping to do so.
>
> I have recently made collections of Agrostis tenuis from a large number of
>
> different lead mines in the nieghbourhood of Aberystwyth and I am hoping
>
> to compare their resistance this winter. (D1041/2/9/19/2)[46]

Indeed, in March of 1953 Bradshaw had collected samples from 20 populations at 14 different sites (D1041/2/9/57). To that collection, Krause contributed samples of *Agrostis* from an old nickel mine in the Black Forest. Yet Bradshaw's plans for the winter of 1954/1955 did not materialize, and would wait for a dramatic scaling-up of the research activities at Bangor within the following two years.

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[46] Bradshaw goes on to write, "The lead mines from which they come are of very different ages, some 50 years old, some 2,000 years old. I am wondering whether they all have resistant populations on them." In his 1952 letter to Nature, Bradshaw wrote that the Goginan mine was "known to be at least a thousand years old." I suspect that these comments are traces of the shift in Bradshaw's thinking toward conceptualizing adaptive evolution as a potentially rapid process.

2.3. Scaling up

In addition to carrying out his teaching duties, and continuing (albeit slowly) his investigation of ecotypic differentiation in *Agrostis*, in 1954 Bradshaw became involved with an erstwhile languishing research project concerning the ecology of hill and mountain grazing in Snowdonia, a mountain park in northwest Wales. Bradshaw's productive involvement with the project would ultimately accelerate the development of his own embryonic research program. Although it is unclear whether the outcome was effected by calculation or by happenstance, erecting a bridge between his own research objectives and the research and management goals of the Snowdonia project pushed the Department of Agricultural Botany toward an emphasis on post-graduate training and research. This would not only move Bradshaw's research forward, but also help to lay the foundation for Bangor's international reputation as a center for plant ecology.

Ecologist R. Elfyn Hughes initiated research at Snowdonia in the 1940s, and was funded by the Agricultural Research Council as part of an effort to increase the productivity of upland pastures for grazing livestock (Hughes 1955). Hughes had studied under R. Alun Roberts, head of the school of Agricultural Botany at Bangor, where he became interested in the history of land use in the Conwy Valley, east of Bangor (Ellis-Williams 1970).[47] After Hughes left the Department for the School of Agriculture at Cambridge in 1949, work on the project continued but at a slower pace. In his 1950 report to the College Council, Roberts lamented an apparent dearth of interest among younger researchers to continue the work in Snowdonia (UCNW Reports of Dept Heads, 1949-50). The project received a jolt of new life in late 1953, when the Nature Conservancy established a National Committee for

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[47] Hughes served as secretary of the British Ecological Society from 1950 to 1956.

Wales, appointing Hughes as Government Protection Officer. This meant that Hughes would spend at least part of his time working from a *pied-à-terre* provided by the Department of Agricultural Botany at Bangor (Report of Dept Heads, 1953-54).

Michael Chadwick, who later worked under Hughes between 1956 and 1959 (see below), described Hughes work and interests at that time:

> If you've got sheep on a mountain, they don't just scatter randomly over the mountain. How much do they graze on the bits which are dominated by, let us just say, by *Nardus*? How much do they graze on the bits that aren't? How much do they on the bits that have got cover grass and how do they move between them from one to the other? How do they move both during the day and from season to season between the higher areas and the lower areas? [Hughes] had an assistant in the Nature Conservancy—he was a more of a warden—out in the field called Evan Roberts. Evan Roberts used to, with binoculars, go and watch sheep on sheep walks. The first person to do this actually was a French-Canadian in Canada who came up and said, "Look, you know, these sheep aren't doing these things randomly. There is an actual pattern to where they go and how they graze." And so Hughes went out and he looked at this and saw that this was true. So then he got Roberts to do quite very detailed recording of where the sheep went […]. I had established some grazing plots in three areas in Snowdonia, and these were open all the year round, open some of the year, or shut. [Hughes wondered], how did the diversity change on these different grazing patterns? (Chadwick 2013)

Whereas Hughes' work focused on patterns of grazing intensity, and the influence of climatic and edaphic factors on overall productivity and diversity, Bradshaw focused his attention on the populations of wild white clover growing in the acidic upper pastures of Cwm Llefrith ("Milky Valley") in southwestern Snowdonia. The valley had long been used for grazing dairy cattle, and (as its named suggests) was known for its outstanding nutritional quality and yield. Applying a transplant methodology similar to the one that he had employed for *Agrostis* in his dissertation research, Bradshaw found that the Cwm Llefrith clover constituted a "distinctive ecological race … characterized by small size but extreme persistence, adapted to upland conditions of grazing and climate" (Bradshaw and Pritchard 1955, p. 596). Writing with Tom Pritchard (Deputy Director of the Nature Conservancy in Wales)[48] in a letter to *Nature* in 1955, Bradshaw hypothesized that the Cwm Llefrith clover was specially adapted to the characteristically acidic, calcium-poor, and magnesium-rich volcanic soil of that area.

The year 1956 was a turning point for Bradshaw in many respects. The previous September he had married Betty Margaret Alliston at Whitchurch in Hampshire (D1041/1/12/1). This meant moving house, and all of the chores and repairs that came along with it. Time for research—already stretched thin by teaching duties—was even harder to find.

Bradshaw's promising but stalled work on lead-tolerant *Agrostis* demanded a new strategy and, combined with the momentum behind his work on *Trifolium* as part of the Snowdonia hill grazing project, made a compelling argument for expanding the research staff

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[48] Pritchard later became widely known for coining the term "environmental education" at a 1948 conference of the IUCN, in Paris.

in the Department. Bradshaw approached Professor Alun Roberts about the possibility of

hiring a post-graduate researcher to move their projects forward. Roberts agreed, and

secured College awards to support two Ph.D. students. One student would help Bradshaw

with his work on lead-tolerance in *Agrostis*, and the other would investigate grasses in the

upland grazings in Snowdonia.[49] The two Ph.D. positions were filled by two of Bradshaw's

Honors students in Agricultural Botany, David "Di" Jowett (b. 14 October, 1934), and

Michael J. Chadwick (b. 1934).

Jowett grew up in a Protestant home in Liverpool (Chadwick 2013), and returned to

Liverpool to work in a sugar refinery during the summers (Jowett pers. comm.,

D1041/2/9/34). As an undergraduate Jowett was drawn to plant breeding, and intended to

find work as such in one of the African colonies. In July, 1956, as graduation drew near,

Jowett made plans to visit the Colonial Office in London to inquire about service overseas.

Meanwhile, Bradshaw had written to Jowett to encourage him to apply for the mineral

nutrition research position, instead. Jowett reported on his trip to London shortly thereafter:

> Dear Tony, Thank you for your letter and for your wife's and your own best
>
> wishes to Pat [Jowett's wife] and myself. I had your letter on the way to the
>
> station to catch the train for London and the Colonial Office, and it was a
>
> heartening thing to have with me. The upshot of the interview was that I
>
> should return to Bangor for three years, or whatever time was necessary,
>
> after which, if I still wanted to enter the Colonial Service my prospects would
>
> be enhanced and I would in any event avoid the two year probationership.

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[49] This was a major turning point for the Department: these would be its first post-graduate
researcher students, paving the way for a rapid expansion of research activities in the
coming years.

This for me was very satisfactory, and I can say quite definitely that I shall be

taking up the Scholarship when it is offered.

That summer, Jowett made weekly trips from Liverpool to Bangor to develop ideas for his

work with Bradshaw, and began working full time at Bangor that fall, supported by both a

government scholarship and a part-time teaching assistantship (Jowett pers. comm.).

Chadwick was born in London, but at the age of five moved south to Guilford with

his parents to avoid the bombings during WWII. At Guilford, Chadwick's parents worked

on a chicken farm owned by one of the conservative ministers of parliament for that region.

Chadwick was interested in both botany and agriculture, and started with Jowett in the

agricultural botany program at Bangor in 1953. In the spring of 1956, Professor Roberts

approached Chadwick about staying on for a Ph.D.. The idea of a moving toward an

academic career appealed to Chadwick, and he accepted.

Chadwick's recollections place his work for Roberts in the context of changes in land

use in Wales, which was a major research priority at Bangor.

Well I was presented with, "Why don't you do a project on *Nardus*?" This

was by Alan Roberts. He had written a paper a few years before […] about

the changing mountains. People were talking about the unchangeable

mountains, you know, there for all time and so forth. But [Roberts] said,

"But of course they're changing tremendously, because land use is changing."

He was interested in land use changes just like [R. E.] Hughes was. And he

said that with the First World War, with the change in family size, people

[…] wanted large joints of meat, of mutton, of small spring lamb and this

kind of thing. And so the whole way in which the farmers in Wales kept their

sheep […] was that they no longer put the sheep on the mountain […] over

the winter: in late October they'd bring them down from the mountain and

they wouldn't put them back up until end of April, early May. And that

meant that by this time the *Nardus* and other species had got rather

unpalatable for them. So that wasn't touched by the grazing very much

anymore and it spread and went out. The work that I did was to show, by

techniques which looked at the sward in quite minute detail, that—although

you couldn't see it—there was actually a pattern developing in the mountains

which was, let's say, 180 centimeters across. […] If you found out—which is

what I did—how quickly it grew, you could say that […] indeed, it did all

start at about the time of the First World War, when all these social factors

began to change so much. (Chadwick pers. comm.).

Although Chadwick was nominally supervised by Alun Roberts, it was R. E. Hughes who

directed his dissertation research. "Alan Roberts wasn't really interested in supervising

people," Chadwick said, "So he kind of farmed this out to the 'Welsh mafia'." (Chadwick

pers. comm.).

A third postgraduate student, Robert William Lodge (1922–21 July, 2008), joined

Jowett and Chadwick in the fall of 1956 with funding from the Canadian government.

Lodge was born in Mulvilhill, in southern Manitoba, about two hours north of Winnipeg,

and spent much of his childhood in Swift Current, Saskatchewan. He attended the College

of Agriculture at the University of Saskatchewan, which was prolonged by military service in

Holland, Italy, and Germany during WWII. After receiving his B. S. in Agricultural Biology,

Lodge accepted a position at the Canadian Department of Agriculture's Experimental Station in Swift Current, Saskatchewan (Lodge 1954).

In 1950 Lodge and his young family moved to Moscow, Idaho, where he pursued a Masters degree under E. W. Tisdale in the School of Forestry at the University of Idaho. Lodge's thesis research focused on the linkages between grazing, soil chemistry (e.g. pH, available phosphorous and nitrogen), and the chemical composition of grasses in the prairies of Saskatchewan. Lodge used exclosures to separate grazed and ungrazed plots on several sites for about twelve months, and found that grazed sites had significantly higher concentrations of phosphorous in surface soils, and that the grasses growing there had significantly higher levels of protein and phosphorous and lower fiber, ash, and ether content (Lodge 1952, 1954). Lodge completed his Masters degree in 1952, and returned to Swift Current as Junior Agrostologist before moving to Bangor in 1956, where he began work on *Cynosurus cristatus*.

A fourth postgraduate student, Roy Snaydon (b. 14 April, 1933), joined the department in 1957. Snaydon had also attended Bangor as an undergraduate, and graduated one year ahead of Chadwick and Jowett. Rather than deferring his two years of obligatory National Service by moving straight into a Ph.D., as Chadwick and Jowett had done, Snaydon decided to complete his National Service before starting a postgraduate program. Bradshaw's genecological work on *Trifolium repens* connected to Hughes' Snowdonia project had attracted interest from the Agricultural Research Council, which provided funding (including a £400 per annum Ph.D. studentship) to conduct a more detailed follow-up study. Snaydon was hired for that work.

A fifth, somewhat enigmatic, postgraduate was involved with Bradshaw's research on metal tolerance: Jean Mary Mobbs (b. 29 September, 1933). Mobbs was an undergraduate in

Neuadd Reichel, where Bradshaw served as tutor, along with Jowett, Snaydon, and Thomas Owen Pritchard (Bangor University Archives, Faculty of Science records). Mobbs was the daughter of Professor Eric Charles Mobbs who served as Chair of Forestry at Bangor from 1947 to 1967. According to Chadwick (2013), Mobbs went on to do a Ph.D. with Bradshaw, probably starting in 1954 or 1955, focusing on *Trifolium repens* and the performance of mixes of other agricultural plants. Mobbs met and married botanist Michael Charles Faraday Proctor (b. unknown) during the course of her degree. Proctor came to Bangor briefly to work for the Nature Conservancy under Hughes after finishing his Ph.D. at Cambridge in 1955 (Proctor, 1955), and prior to accepting a Lectureship at the University of Exeter in November, 1956 (Proctor, 2015). It is unclear whether Mobbs completed her Ph.D., since there is no record of a dissertation under the names Jean Mobbs or Jean Proctor at Bangor.

The influx of postgraduate researchers was a sea-change for the Department of Agricultural Botany. Although the Department of Botany regularly supported as many as five postgraduate students, the Department of Agricultural Botany had focused almost exclusively on undergraduate training, especially aspiring plant breeders (UCNW Reports of Department Heads). A great deal of responsibility for moving Bangor into a more prominent position as a center for plant sciences lies with Bradshaw. "I think [that Bradshaw], in a sense, saw it as his job that he should be encouraging things like [recruiting postgraduate researchers] in the department, in the sleepy, small department, which hadn't done a great deal," Chadwick (pers. comm.) recalls, "Bradshaw out of all of the people was the high flyer. […] He was the enthusiast, the one that made the most noise, did most, had far more connections outside Wales and the department, from Cambridge […] and Aberystwyth […]. He was more of the mover and shaker" (Chadwick pers. comm.).

Figure 2.3.1. Inside the greenhouses at UCNW Bangor.

Bradshaw and the new cohort of postgraduates formed a cohesive research group, with Bradshaw acting as cheerleader (UCNW Report of Department Heads, 1956–1957).

[Bradshaw] drives a lot of the discussion with ideas. He's enthusiastic. He's got a lot of imagination and he enables you to do things. He's an enabler. I mean he's not the kind of person that says, "Well I don't think you want to do that because I'm doing it." You know, he's the "well I was thinking of doing that but why don't we all do it together" type. So he was somebody who encouraged and helped and -- I mean it's not too strong a word to say that he did inspire you with ideas. (Chadwick pers. comm.).

Although the four postgraduates focused on different plant species, and had somewhat different research questions,[50] they quickly found a common interest in the response of their respective plant species to various soil nutrients.

Meanwhile, Bradshaw's work on *Agrostis* had inspired another young genecologist, Dennis A. Wilkins, at the SPBS. Wilkins set out to replicate Bradshaw's discovery of tolerant *Agrostis* on the tainted soils of Leadhills in southern Lanarkshire (D1041/2/9/23), infamous for lead mining operations dating to the early 17th century (Bartholomew 1904, p. 482). Although Wilkins was unable to find a tolerant variety on the Leadhills mines, despite an abundance of the grass in nearby pasture, he did find the closely related *Agrostis canina* growing on a zinc mine. He also found a great deal of *Deschampsia flexuoso* and *Festuca ovina* on lead-contaminated soil, and by autumn of 1956 preliminary results from greenhouse trials indicated that those local *F. ovina* plants were indeed more strongly resistant to lead nitrate than their conspecifics found on normal soil. He also found *Agrostis* growing near an old zinc mine, and hypothesized that *Agrostis* species were uniquely capable of producing a zinc-resistance ecotype, while *Deschampsia* and *Festuca* could uniquely develop a resistance to lead (D1041/2/9/23). Wilkins' findings exacerbated the need for detailed characterization—what Bradshaw called "direct evidence"—of responses to specific soil factors.[51]

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[50] Jowett: *Agrostis* and *Anthoxanthum*; Chadwick: *Agrostis* and *Nardus*; Snaydon: *Trifolium*; Lodge: *Cynosurus*.

[51] In September, 1956 a group from the SPBS, including Gregor, Gregor's long-tim research partner Patricia Watson (who had also begun work on Agrostis), D. J. Harberd, and Wilkins visited the Grass Breeding Unit at the WPBS, giving Wilkins an opportunity to meet with Bradshaw to discuss their findings. Meetings between the Edinburgh, Aberystwyth, and Bangor genecological and plant breeding groups would become an annual affair, growing into what is today a highly respected (if small) association of the British Ecological Society, known as the Ecological Genetics Group.

In July, 1956, members of the Welsh Plant Breeding Station—including director E. T. Jones and cytologist Keith Jones—traveled to Cambridge for the annual meeting of the Fellows of the National Institute of Agricultural Botany. The WPBS had realized great success in developing new varieties of winter oats, and E. T. Jones was honored at the meeting with NIAB's Cereal Award for his new 'Powys' variety. NIAB and the WPBS had been cooperating closely, and were in the process of transferring responsibility for the production of Aberystwyth grass and clover stock seeds to NIAB.[52] James Gregor from the SPBS was also in attendance, and during a lengthy discussion with Keith Jones expressed his desire to organize a joint meeting between the two Stations that might appeal more directly to their mutual interests (Harberd pers. comm.). In particular, Gregor wanted to facilitate a meeting between Dennis Wilkins and Bradshaw, and to visit some of the mine tips where Bradshaw had found locally adapted populations of *Agrostis*. In late September, 1956, a delegation from the SPBS—including Gregor, Wilkins, Patricia J. Watson, and David J. Harberd—met with Bradshaw, Keith Jones, and others of the WPBS staff. This meeting was the first of what would become the annual Ecological Genetics Group meeting, a special interest group of the British Ecological Society and a celebrated fixture of the ecological profession now in its 57th year.

The timing of Wilkins' and Bradshaw's acquaintance in the autumn of 1956 was opportune, as it facilitated collaboration on a method for more precisely identifying the soil factors to which various ecotypes of grasses and clover might be adapted.

Especially because the differential survival of *Agrostis* varieties on contaminated soil seemed to involve differences in root growth, Bradshaw focused on developing an

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[52] "National Institute of Agrilcultural Botany, Cambridge, Report for 1956." *Nature* 178: 529.

alternative to Keaton's lead-treatment assays that would allow more efficient access to roots. With Mobbs' assistance, Bradshaw developed a sand culture technique that involved planting tillers on sterilized quartz sand to which was added various culture solutions (Mobbs and Bradshaw 1957, Bradshaw *et al* 1958). This removed the messy and error-prone process of extracting plants from soil: the quartz sand could easily be washed away without damaging the roots. Bradshaw described the earliest sand culture experiments in his notes:

> We found we were all interested in the soil nutrient factors to which our
>
> different species might or might-not be adapted—several people including
>
> Alun Roberts had surmised from the field that they might be very different
>
> but there was no direct evidence so we set up a series of large sand culture
>
> experiments to test this, involving 5 or 6 species, 4 or 5 nutrient levels and 3
>
> replicates. These had to be watered every day with culture solutions without
>
> making mistakes. We found this was not easy. It was the big mistakes which
>
> were the problem, so we devised elaborate colour codes for the different
>
> concentrations. We also an elaborate cocktail bar system for ensuring the
>
> solutions got made to the right strength. This taught all of us a lot about
>
> achieving accuracy in ordinary experiments." (D1041/13/2/9)

Wilkins took the Bangor group's method one step further, dispensing with sand altogether and growing tillers directly on tubes of aqueous nutrient solution. Wilkins' trials with the *Festuca* that he found on a mine-tip in Leadhills suggested that not only were those tolerant plants specifically resistant to lead, but that increasing the concentration of calcium

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in the nutrient solution could reverse the toxic effects of lead on non-tolerant plants.[53]

Jowett adopted and refined Wilkins' method for use with the mine populations of *Agrostis*, and both the sand- and water-culture techniques became a central part of both Wilkins' and the Bangor team's research program.

In light of Wilkins' results, as well as questions from the Snowdonia hill grazing project about adaptation to acidic upland soils, the Bangor group focused its efforts on the reaction of local populations of grasses and clover to pH, nutrients such as calcium and phosphate, and a wide range of heavy metals associated with volcanism and the mine dumps. The Bangor group supplemented the mineral cultural assays with experimental plants, testing local populations from a growing array of grass species.

The energy and determination of the young research group at Bangor was not only invigorating, but it also gave Bradshaw the breathing-room he needed to finish his dissertation in 1959, and to begin publishing the results of his extensive study of local adaptive differentiation in *Agrostis* (Bradshaw 1959). It also enabled him to wrap up his work with Ellis Davies on hybrid *Agrostis* from Port Meadow, Oxford, (Bradshaw 1958b, d) and to develop certain ideas about adaptive phenotypic plasticity that had been simmering in his mind since 1954 into an empirical research program.[54]

It was not long before the question of specificity in the metal-tolerant *Agrostis* was more-or-less settled. Using both the sand- and water-culture protocols, the Bangor group was able to precisely identify the soil factors to which different populations of *Agrostis* were

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[53] Wilkins, D. A. 1957. "A Technique for the Measurement of Lead Tolerance in Plants." *Nature* 180 (4575): 37–8.

[54] Bradshaw conducted a series of greenhouse experiments, starting in 1957, aimed at investigating phenotypic plasticity as an adaptive trait in local populations of plants.

tolerant, using root growth as a metric. Bradshaw wrote to Kruckeberg again in September of 1958, announcing that: "There is no doubt that in contrast with your serpentine populations these populations are directly resistant to the heavy metals concerned rather than being adapted to low phosphate levels" (D1041/2/9/26). Indeed, populations of *Agrostis* growing at nickel mines showed specific tolerance to nickel, those growing on copper-contaminated soil showed specific tolerance to copper, and the Goginan population did in fact show a specific tolerance to lead, ruling out Newton's phosphate-deficiency hypothesis.

The complex patterns of specific adaptation to soil factors over micro-geographic scales that was emerging from the Bangor group's research put meat on the bones of Gregor's rejection ecotypes as discrete entities (section 1.2.4). In 1959, Bradshaw wrote, "it is clearly not possible to delimit ecotypes, ecodemes or other units in *A. tenuis* without being subjective. Since there are no discontinuities it is utterly impossible to decide where one unit begins or ends" (Bradshaw 1959, p. 225). Instead, Bradshaw conceptualized the distribution of genetic variation in a population as a system of "graded patchworks:" (Bradshaw 1960) "clines of varying slopes interspersed with rather sharp discontinuities corresponding to changes in the environment" (Jain and Bradshaw 1966). Bradshaw saw differentiation in each of a plant's physiological and morphological characteristics as a product of specific selective pressures in the environment, which may or may not be related.

The extent to which the British style of genecology practiced by Gregor and Bradshaw had diverged from that of the California school is highlighted by a letter from Jens Clausen to Bradshaw in 1960. As I mentioned above, David Keck had already expressed skepticism about whether the differences that Bradshaw found between populations of

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Agrostis tenuis were real or biologically meaningful. Clausen's remarks were somewhat more positive, noting that "the inter-population variation [described in Bradshaw (1959)] follows a similar pattern to what we have observed in California" (D1041/5/1/1/17). But Clausen's subsequent comments show deep differences in thinking about the nature and significance of those population differences.

Clausen objected to the idea that Bradshaw had found ecotypic differentiation in relation to climate, on the grounds that there was simply insufficient variation in climate across Bradshaw's sampling sites to generate distinct ecotypes.

> The discussion on ecotypes and on taxonomy in your October 1959 paper…has me confused, because, as far as I can see, the area that has been sampled is climatically so uniform that no climatic ecotypes should be expected to exist. […] It may come as a shock to you, but I have a suspicion that except for the Scottish mountains and the exposed northwest shore the major part of the island of Great Britain probably belongs to one climatic zone, just as in California the outer Coast Range constitutes one ecological zone characterized by the mixed evergreen forest. (D1041/5/1/1/17)

Moreover, for Clausen ecotypic differentation concerned discontinuities in heritable variation that were much broader than the inter-population differences on which Bradshaw focused.

> I notice that my British genecologist friends constantly look for distinct climatic ecotypes in Great Britain and become confused because what they find is only the erratic variation between local populations. […] Differences between climatic

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ecotypes are of a higher order than differences between populations.

(D1041/5/1/1/17–18)

This passage shows clearly that Clausen and the other California genecologists thought about ecotypic differentiation on a much larger scale than Gregor, Bradshaw, and their colleagues. Clausen's ecotypes were concerned with environmental and genetic differences of a much greater magnitude and on a much larger spatial scale compared to Gregor and Bradshaw's concept of ecotypic differentation. Whereas Bradshaw and Gregor were more concerned with the "graded patchwork" of differentiation in individual characters on small spatial scales, the California school remained committed to a theory of discontinuous ecotypes differentiated on the basis of multiple characters across large geographic regions.

Starting in 1958, the tight-knit mineral nutrition group began to go their separate ways. Bob Lodge finished his dissertation in 1958, and returned to the Research Station at Swift Current. In 1964 the United Nationals Food and Agriculture Organization hired Lodge for an eighteen month stint in Lahore, Pakistan. Lodge worked in the Canadian agricultural research sector for the remainder of his career. Di Jowett and Mike Chadwick both finished their degrees in 1959. Jowett's career turned largely toward statistics, and after working at the University of Iowa for several years he accepted a tenure-track position at the University of Wisconsin at Green Bay where he remained for the duration of his career. Chadwick spent a short period at the University of Khartoum, and several years in the School of Agriculture at Cambridge, before joining the Biology department at York in 1966. Roy Snaydon finished his degree in 1961, and went on to a post-doctoral position at Reading. Snaydon, who remained involved with the work on mineral nutrition and local adaptation, remained at Reading for a large part of his career.

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With the retirement of Professor R. Alun Roberts on the horizon, in 1958 Bradshaw made an application to the College for the Professorship of Agricultural Botany (D1041/13/3/49). Bradshaw was in the final stages of preparing his dissertation—he submitted his application to graduate at about the same time as he submitted the application for the Professorship—and had already amassed an impressive collection of publications. Roberts, Paul Richards, and Herbert Baker,[55] served as referees. Despite Bradshaw's productive and expanding research program, and his record of service to the College, Oxford-trained ecologist John Lander Harper was chosen to fill the post instead. Perhaps an aspiration toward a full Professorship was premature, despite a portfolio of almost twenty research publications, as he would have only just received his Ph.D. upon assuming the post. In 1959 Bradshaw interviewed, also unsuccessfully, for a University Lectureship in Agricultural Botany at Cambridge (GD449/16/15).

While Bradshaw's attempt at the Professorship was unsuccessful, his application provides a unique window into his research priorities at that time, as well as his perspective on the relationships between ecological and agricultural research:

Should my application be successful, I would hope to continue the ecological

tradition of the department. Ecology provides a central focus of agricultural

and botanical studies from the point of view of both teaching and research. I

would like in particular to develop the experimental side of this subject and

to link such work with both physiology and crop husbandry. There is

considerable scope for both research and teaching in this field.

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[55] Who had meanwhile accepted a position at the botanical garden at the University of California, Berkeley.

From a more general point of view, I believe that the most important

aspect of Agricultural Botany is where it can show the value of bringing

theoretical, botanical discipl[in]es to bear on practical agricultural problems. I

am therefore convinced there should be close contact between theory and

practice, whether it be between genetics and plant breeding, physiology and

crop husbandry, mycology and disease control, or ecology and cropping.

Bangor provides ideal opportunities for such an approach and I would like to

encourage it in both teaching and research. (D1041/13/3/49, p. 3)

Bradshaw's brief manifesto leaves little doubt that the agricultural context in which

Bradshaw's graduate training and early research took place was more than an arbitrary

backdrop for an otherwise purely intellectual initiation.

Despite losing out to Harper for the Professorship, Bradshaw would continue to

develop the growing research program at Bangor.[56] This included training graduate students

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[56] Bradshaw would remain watchful throughout the 1960s, anticipating his next career move. When the University of East Anglia was created in 1962, Bradshaw probed the possibility of a move that would bring him closer to "long standing connections with Norfolk and Norwich." (D1041/13/3/46). Probably unbeknownst to Bradshaw, noted Edinburgh geneticist Conrad Hal Waddington had recently been involved in a heated and controversial bid for the position of Vice-Chancellor at East Anglia, which finally fell apart in the summer of 1961 over issues of salary and research funding. No suitable position for Bradshaw materialized, but he was promoted to Senior Lecturer at Bangor that winter (D1041/13/3/43/2; D1041/13/3/3/2). In 1963, he turned down an offer to replace the ailing Wendell H. Camp as head of the Department of Botany at the University of Connecticut, fearing that the research community would lack the energy of the one that he had helped to cultivate at Bangor, and uneasy about the "Americanisation" of his three young daughters, Jane, Penny and Sarah (D1041/2/9/31/1). As Bradshaw put it, he preferred to "stay on happily trying to improve old Britain, rather than desert it for somewhere else!" (D1041/13/3/45/2). He also resisted the courtship of Richard Lewontin at the University of Chicago several years later (D1041/13/2). Bradshaw was promoted to Reader in 1964 (D1041/13/3/50), and finally left Bangor for the University of Liverpool in 1968, where he took over as Professor of Botany. In 1970, two years after

from Africa and Asia, brought to Bangor through programs like the Sir William Roberts scholarship.[57] When Harper arrived at Bangor in 1960, after a sabbatical year at the University of California Davis, a vibrant research community was already germinating in the Department of Agricultural Botany.

The first phase of Bradshaw's research program had addressed some of the core questions of Gregorian genecology: to what extent are populations *Agrostis tenuis* ecotypically differentiated in relation to edaphic gradients, in what characters is such differentiation manifest, and what are the specific environmental and physiological factors involved? A variety of other questions, however, continued to occupy Bradshaw's thoughts (D1041/2/9/52). For example, he wondered about the "genetics of resistance:" was tolerance of the mine soil a dominant or a recessive trait? Was it controlled by a single gene, or many? With Snaydon's help, Bradshaw had begun controlled breeding experiments with locally adapted populations of *Festuca* to explore the potential for commercial development, but in 1960 it was too early to draw conclusions. Bradshaw also wondered about the genetic composition of both adult plants and seeds around the mine boundary: what was the degree of heterozygosity for resistance-conferring genes in the population of *A. tenuis* surrounding the mines? Was there significant gene flow from the non-tolerant segments of the populations into the contaminated soil? Could differences in the average tolerance of

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accepting the professorship in Botany at Liverpool, Bradshaw was courted by the University of Chicago, a match for which noted American population biologist Richard Lewontin strongly lobbied (D1041/13/3/25). Bradshaw turned down the Chicago offer, as well.

[57] A scholarship program started by Sir William Roberts, used to send Pakistani students from the area of Khanewal, in the Punjab Province, to receive graduate training in agricultural botany at Bangor. Bradshaw supervised many of the students who came to Bangor through that program in the late 1950s and 1960s.

seedlings and adults on the contaminated soil provide an indication of the "power of selection" at work? Bradshaw had noticed that individuals from the tolerant populations tended to grow less vigorously than their non-tolerant counterparts when planted on uncontaminated soil. Just how much gene flow *off* of the mine soil was taking place? Was there selection acting *against* those tolerant emigrants? Finally, given all of those potentially important factors, what conditions were necessary for tolerance to emerge in the first place? Bradshaw surmised that this might depend on the presence of that character at low frequencies in nearby populations, and wondered whether it was possible to isolate tolerant individuals from populations of *Agrostis* growing many miles away from the mine. Many of these questions would dominate Bradshaw's research efforts, and those of his growing community of graduate students, in the 1960s.

2.3. Quantification

During the 1950s Bradshaw and his students produced a compelling body of research that demonstrated genetic differentiation in plant populations on extremely small spatial scales. Their work on mineral nutrition showed that such differentiation was highly specific: local populations were adapted to individual toxins or mineral deficiencies in the contaminated soils around old mines. Bradshaw and his students had stabilized a phenomenon that pushed the extremes of Gregorian genecology in terms of both its locality and its specificity. It seemed obvious to Bradshaw that differentiation on the mine tips was the result of powerful and ongoing natural selection. *A. tenuis* was an obligate out-breeder, and the distances over which differentiation was occurring were so short that a substantial amount of gene flow, which theory said should dampen differentiation, must be taking place. Bradshaw had observed early on that the lead-tolerant *A. tenuis* performed relatively poorly on uncontaminated soils, stacking the deck further against the success of tolerance-conferring

genes in the mine-tip populations. The only reasonable conclusion seemed to be that natural selection was extremely strong, and that differentiation on the mines was perpetuated by the interplay of evolutionary forces on a year-by-year basis.

The final transformation in Bradshaw's investigative pathway was to scrutinize directly those evolutionary forces. By the end of the 1960s, Bradshaw's research program had transitioned from a study of hereditary variation in plant populations—providing an increasingly fine-grained picture of genetic differentiation in relation to patterns in the environment—to a quantitative investigation of evolutionary dynamics in real time. That investigation was comprised of three main activities: (1) characterizing the magnitude and dynamics of gene flow on small spatial scales, (2) quantifying natural selection in natural populations, and (3) performing computer simulations that incorporated quantitative models of gene flow and selection.

2.3.1. Gene Flow and Selection

The potential for interbreeding within and among plant populations played an important role in the genecological theoretical framework from its inception by Turesson in the 1920s. The ability of populations to interbreed was the primary criterion for delimiting ecospecies, which is the major reason why cytology was so significant for genecological research: at the time, ploidy difference were seen as one of the main barriers to interbreeding among conspecifics. In Gregor and Sansome's work on *Phleum* in the 1920s, for example, their delimitation of ecospecies was based on differences in chromosome number. When Bradshaw consulted Gregor about his dissertation research in the late 1940s, Gregor advised him to make some account of the "breeding potentialities" of his populations of *Agrostis tenuis* and *Anthoxanthum odoratum*. Interbreeding was an important part of the Mendelian

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interpretation of Darwinian evolution in the early 20th century: if the unit of evolution was the panmictic population, then evolutionary divergence would depend primarily on the introduction of barriers to reproduction.

Bradshaw's interpretation of the situation at Goginan and other mines was that selection for resistance was so strong that it overrode the equalizing effect of genetic admixture with the local grass populations. This view was bolstered by work by D. J. Griffiths in the Grass Breeding Department at the WPBS on cross-contamination in varietal trials and seed multiplication. Griffith's (1950) data suggested that a planting distance of 100 yards would keep cross-contamination below 2%. If gene flow could attenuate to such a marked extent over a short distance, it would make it even easier for selection to maintain a high frequency of tolerant plants in proximity to non-tolerant populations. Bradshaw's interpretation was also strengthened by Jowett's analysis of samples along a transect perpendicular to mine boundaries, which showed that there was a sharp shift in the proportion of tolerant individuals around the edge of the contaminated soil despite a continuous distribution of plants.

Some of the earliest quantitative studies of gene flow on the mine tips were carried out by Bradshaw's student Janis Antonovics in the mid-1960s. Antonovics was born in Riga, Latvia in 1942, and spent much of his childhood in Kent, U.K. In 1963 he graduated from Cambridge, where he studied botany and genetics. In 1963, Antonovics commenced his Ph.D. research at Bangor under the joint direction of Bradshaw and Harper. Antonovics' interest in the interplay of selection and gene flow was piqued by John Thoday at Cambridge, who encouraged Antonovics to go on to work with Bradshaw. "The main thing that I got interested in in Thoday's department was disruptive selection and speciation,"

Antonovics later recalled, "It was Thoday that recommended I go and work with Bradshaw, because Bradshaw had been showing this very sharp differentiation at metal mine boundaries. Thoday had heard [Bradshaw] talk at conferences [see chapter 3], and maybe some of the early work had actually been published. [Thoday] said if I was interested in plant evolution, I should think of working with Bradshaw" (Antonovics pers. comm.). When Antonovics arrived at Bangor in the autumn of 1963, however, Bradshaw was away on sabbatical at UC Davis, so Harper helped to guide Antonovics in the early phases of his project.

The full extent of Antonovics' early research at Bangor goes beyond the scope of the present dissertation. But his ideas about its main contours at the start of his program in 1963 gives a good indication of the major direction of the Bangor group's investigations. In November 1963, Antonovics sent Bradshaw a draft prospectus for his research over the next few years. The main focus of that prospectus was (1) clarifying the genetics of metal tolerance—how many genes were responsible for the tolerance, what was the degree of heterozygosity in mine populations for those genes—and (2) characterizing the extent and spatial parameters of gene flow (in form of both seeds and pollen) in the populations around the mines (D1041/5/2/1/42).

One of Antonovics' ideas for characterizing pollen flow involved planting an albino form of *Agrostis stolonifera* at the boundary between contaminated and uncontaminated soils. Several non-albino *A. stolonifera* would also be planted at varying distances from that "source" plant. Assuming that albinism was determined by a single gene (June Archer, an undergradaute honors student in Agricultural Botany, was investigating this), and that both the albino "source" and non-albino "sink" plants were self-incompatible, then the number of seeds collected from the "sink" plants would give an indication of the extent of pollen

flow onto the mine tip at various distance. "It never worked," Antonovics later recalled. "We ended up measuring gene flow physically, actually, by putting out glass slides with Vaseline
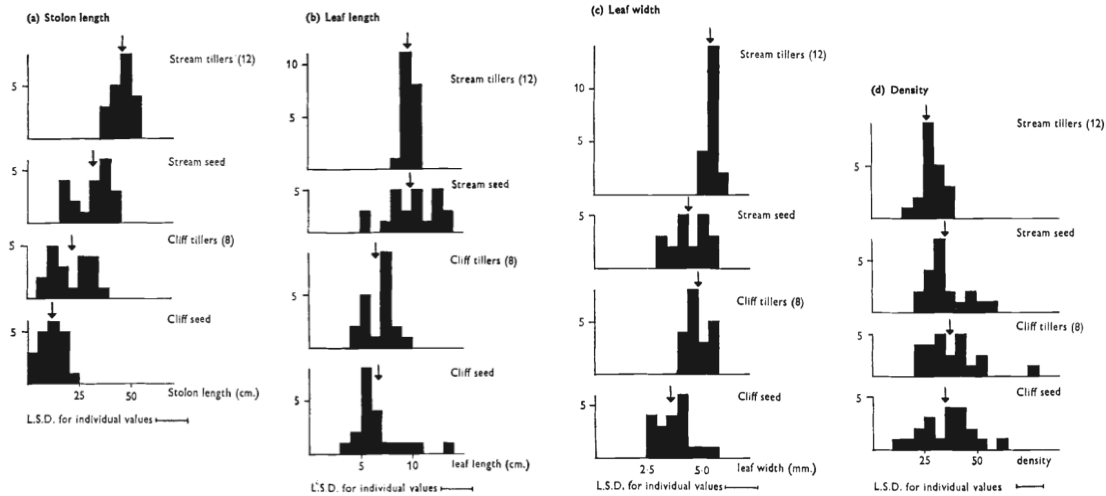
Figure 2.3.2. Differences in genetic variation from seed and tiller samples at contrasting sites at Abraham's Bosom. Figure 4 in Aston and Bradshaw (1966, p. 657).

on it at different distances" (Antonovics pers. comm.).

Antonovics, Bradshaw, and several other of Bradshaw's students at Bangor— including Tom McNeilly, Peter Kyle, J. L. Aston, R. P. G. Gregory, and Mohammed Akram Khan—carried out a wide variety of selection experiments on "artificial" mines in the mid-1960s. These experiments involved sampling widely from non-tolerant populations of *Agrostis*, *Anthoxanthum*, *Holcus*, and other species around the mine tips, and then cultivating those samples on contaminated soils to see how quickly tolerance could evolve. In several cases it took only a few generations for an essentially non-tolerant artificial population to adapt to the contaminated soils. On the mine tips, the Bangor group worked to characterize differences in survival. Antonovics work also showed that differences in flowering time over small spatial scales helped to reinforce the adaptive divergence of tolerant plants by restricting gene flow.

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For much of the 1950s, Bradshaw had used relative vegetative growth as a proxy for the "selective values" of individual plants. Reviewers of Bradshaw's manuscripts were skeptical of this approach, and in the mid-1960s Bradshaw and his students used a different approach. In Chapter 1, I mentioned that Gregor decided to sample seed rather than tillers in his genecological studies of pasture grasses. Other genecologists, including Bradshaw, relied on vegetative cuttings. In 1953, David Harberd proposed a method for determining whether or not tiller-sampling resulted in an adequate representation of the genetic variation in populations. The basic idea was to sample both seed and tillers from some locales, and then compare the distribution of character variation in plants raised from the two sets of materials. Bradshaw implemented this method in his genecological work in the 1950s. In the 1960s, however, Bradshaw reinterpreted the significance of Harberd's method: by comparing the distribution of variation in samples from seed and from tillers, Bradshaw reasoned, one could infer the magnitude and direction of natural selection acting on a population.

One example of the seed-tiller method of quantifying the magnitude and direction of selection can be found in Aston and Bradshaw's (1966) study of *Agrostis stolonifera* along the shoreline at Abraham's Bosom, a rocky bay on Anglesey to the northwest of Bangor. Aston and Bradshaw sampled from thirteen sites along a transect perpendicular to the shoreline: from the bottom of the sea cliffs and into the pastures above. Plants on the cliff tended to adopt a dwarf growth form, with smaller leaves and shorter stolons, whereas plants closer to the stream in the nearby pasture had a more upright form. By sampling both seed and tillers at each station, Aston and Bradshaw were able to show the difference between the total genetic variation available at each site and the range of variation that was actually able to survive (Figure 2.3.2).

One of the most dramatic methodological shifts in Bradshaw's work during the 1960s was

his use of computer models to study gene flow and selection in hypothetical plant

populations. Bradshaw's first foray into such computer models occurred while he was on

sabbatical at the University of California at Davis in late 1963 and early 1964, working with

plant population geneticist Robert W. Allard (see chapter 3). Bradshaw also began

collaborating with Indian theoretical population geneticist Subodh K. Jain, leading to a co-

authored publication in 1966.

Jain and Bradshaw's computer model simulated changes in gene frequencies in a

series of sub-populations as a product of natural selection and gene flow. The model

assumed that ten infinitely large, partially isolated sub-populations lay along a linear transect,

with five sub-populations on each side of a sharp boundary between two environments.

Each environment featured a different set of selective pressures with respect to a

dichotomous character (e.g., tolerance to a toxic metal). Each simulation started with one

allele at a very low frequency in the population, and ran until gene frequencies stopped

changing, or 250 generations had passed. Upon each run of the simulation, they manipulated

certain parameters: the distribution of gene flow, the relative generation times of populations

in each environment, the "selective values" of each allele in each environment, and the

degree of dominance of the initially-rare allele.

Each run of the simulation produced three results: a distribution of gene frequencies

across the 10 serial sub-populations, the variance of that distribution, and a statistical

measure of differentiation, E, based on variance and the average gene frequency (Jain and

Bradshaw 1966, p. 422). In their eventual publication, Jain and Bradshaw presented the

distribution of gene frequencies graphically, as shown in figure 3. They reported average

gene frequencies, variance, and differentiation as tables of numerical values in relation to

various selective values, dominance, relative generation times, and gene flow models.

Jain and Bradshaw used a collection of gene flow models drawn from both theory

and experiment. In order to study the potential for random sampling to produce genetic

differentiation in finite sub-populations, Sewall Wright and Motoo Kimura had introduced

discrete models—known as "island" and "stepping stone" models—that treated populations

as sets of separate sub-populations between which finite amounts of gene flow could occur.

In other cases, population geneticists had modeled gene flow using a normal distribution,

with exchange between locales tapering continuously with distance.

To this collection, Jain and Bradshaw added a model of gene flow based on a

leptokurtic distribution.[58] Whereas the other gene flow models were drawn from theory (the

normal curve likely having been preferred by theorists for reasons of computational

convenience), Jain and Bradshaw's choice of a leptokurtic model stemmed from

experimental work by plant breeders and ecologists. In the late 1940s, David Griffiths at the

WPBS conducted a series of experiments to study the effect of isolation distance on

hybridization between bred varieties of ryegrass (Griffiths 1950). A. J. Bateman at the John

Innes Horticultural Institute had carried out similar experiments using beets and maize

(Bateman 1947). They both found that the extent of gene flow between plants tapered with

distance far more rapidly than could be represented with a normal curve. Although one of

Bradshaw's students, Tom McNeilly, had begun to implement Bradshaw's 1956 prescription

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58 A leptokurtic distribution is one in which the majority of variance is due to a very small number of
    extreme outliers: a leptokurtic curve is therefore steeper than a normal curve, with a greater
    concentration of cases situated closer to the mean.

for estimating gene flow by comparing seedlings and adults, his results were so far quite tentative.

In order to simulate the effects of natural selection on gene frequencies, Jain and Bradshaw drew on theoretical resources from population genetics, and a choice of selection coefficients consistent with the view of selection that Bradshaw and his students had adopted. In keeping with the conventions of population genetic theory, the relative reproductive fitness of each genotype was calculated as a function of both dominance and "selective value," represented as the fractions **h** and **s**, respectively.[59] They modulated dominance between complete (**h**=1) and partial (**h**=0.5). Jain and Bradshaw's choice of selective values certainly reflected Bradshaw's aspiration toward a synthesis of theoretical population genetics with genecology, and his view that natural selection could act with significant power to shape populations. While still at Davis in 1964, Bradshaw wrote:

> It is...surprising that in theoretical studies the coefficients of selection that have been used most widely have been .01 and .001. Unwittingly, the use of these figures has done a disservice to the study of evolution in suggesting that natural selection usually does not give more than 1 per cent selective differential; that is clearly nonsense and is now being corrected. (Bradshaw 1964)

Accordingly, Jain and Bradshaw used selective values no smaller than 0.10, and as high as 0.95.

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59 This will be familiar to anyone who has taken an introductory genetics course. In a given environment featuring selection favoring an allele, A, the fitnesses of the three possible genotypes at that locus are calculated: *AA*: 1; *Aa*: 1 - *hs*; *aa*: 1 - *s*, where **h** is the fractional degree of dominance of *A*, and **s** is the fractional coefficient of selection against *a*.

The most blatantly counterfactual assumption of Jain and Bradshaw's simulation model was that each sub-population was composed of an infinitely large number of individuals. Such counterfactual assumptions were not uncommon in theoretical population genetics: the Hardy-Weinberg equilibrium model, for example, similarly assumed that population size is infinite. Philosophers and biologists have defended the use of such universally false assumptions, arguing that when used appropriately such assumptions can simplify a model sufficiently to generate useful insights about other features in the model (Levins 1966, Plutynski 2001, Winsberg 2012). In this case, the assumption of infinite sub-population size was intended to stabilize the simulation against "random differentiation:" sub-populations of finite size would be subject to a certain amount of gene frequency change merely as a result of sampling, obscuring the effects of selection and gene flow.

By the time that Jain and Bradshaw began publishing the results of their simulation in 1966, a dominant theme in their presentation was the apparent paradox of genetic differentiation in the presence of substantial gene flow. Despite what Bradshaw considered to be "undeniable evidence that populations occupying contrasting closely adjacent habitats can become differentiated from each other," the idea that strong selection for tolerant varieties was sufficient to overcome the swamping effects of gene flow on such small spatial scales was "doubted on intuitive grounds by many investigators" (Bradshaw 1966). This was exacerbated by the popular view that geographical isolation was necessary for sustained evolutionary differentiation. Even if Bradshaw could produce tolerant varieties of *Agrostis* in an artificial selection experiment,[60] he remained vulnerable to the rebuttal (popular at the time) that although such a scenario was possible in principle, it could hardly be said to occur

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60 An experiment which, shortly thereafter, he and students did successfully carry out.

frequently, and was therefore insignificant—and Bradshaw was certainly convinced that such a scenario was both frequent and significant. In this light, the simulation model could be construed as providing what Anya Plutynski has called a "plausibility argument:" demonstrating that a particular evolutionary mechanism *could* have been involved, despite a lack of direct evidence that it was *actually* involved (Plutynski 2001).

I think that it would be a mistake, however, to construe the epistemic role that the simulation was designed to play in terms of the claims in support of which it was later marshaled. There are a few reasons to be skeptical of such a conflation.

First, it is clear that there was no sense in which Jain and Bradshaw intended the execution of the simulation as a test of theory by comparison to empirical data, even if the simulation could be construed as a complex hypothesis about the causes of microgeographic differentation. The principle outputs of the simulation were gene frequencies, variance in gene frequencies, and E—an index of differentiation based on gene frequency variance. Jain and Bradshaw had no access to these parameters empirically. The genetic basis of metal tolerance was largely unknown, with only tentative indications from research in other species that such a character might be dominant. The comparisons that Jain and Bradshaw did make between the results of the simulation and empirical data were qualitative at best, based on the loose assumption that mean tolerance was an indicator of gene frequency. Likewise, the simulation was not a mere extrapolation of experimental results. Although the selective values used in the model were of the same order of magnitude as those estimated based on differential growth in reciprocal transplant experiments,[61] had they intended to closely

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61 Bradshaw and Jain did receive some resistance from the editor of Heredity concerning their estimates of coefficients of selection against "unadapted types." They had estimated the coefficients using data from reciprocal transplant experiments. They compared the vegetative growth (as dry weight) of individuals
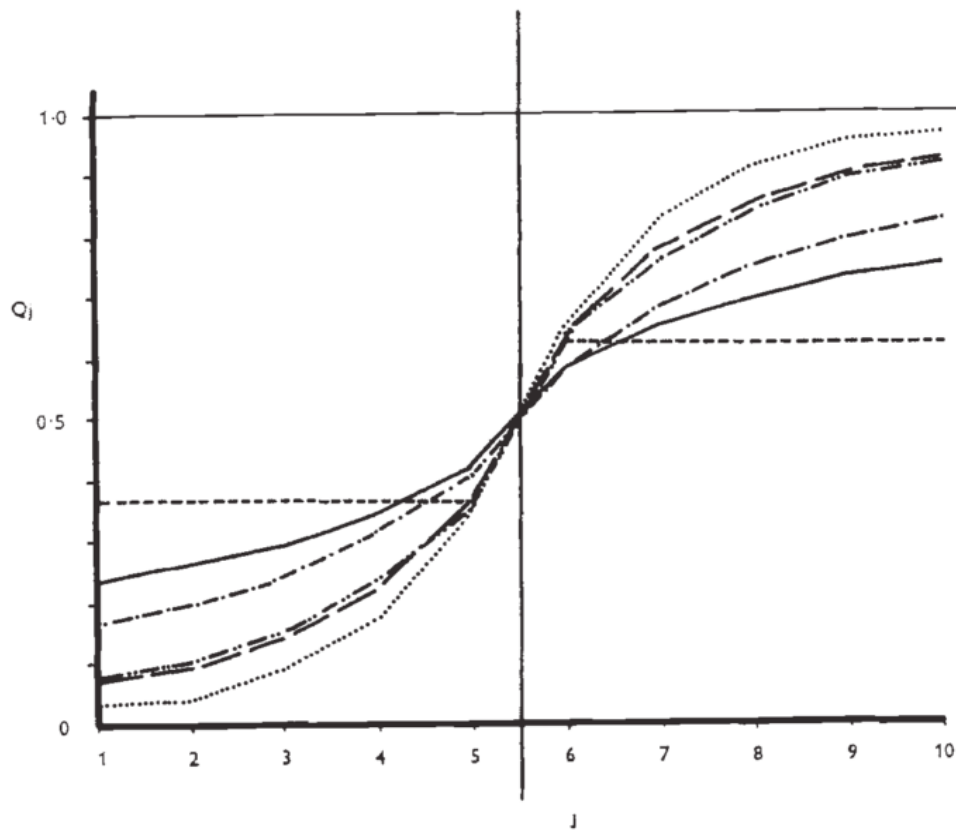
(c) $s_1 = s_2 = 0.25$; $t_1 = t_2 = 1$

Figure 2.3.3. Sample output from a series of simulation runs. Selection is symmetrical: the intensity of selection for or against the rare allele has equivalent magnitude in each environment. Generation times in each environment are identical. Each line depicts the distribution of gene frequencies (Y-axis) across each of the ten serial sub-populations (X-axis) for one of the six models of gene flow. (Jain and Bradshaw 1966; p. 427).

represent particular cases in the model they could easily have plugged-in experimentally-

derived estimates, yet they did not.

Second, interpreting the simulation as an attempt to accrue support to the claim that

the patterns of differentiation found at Goginan and other locales was caused by strong

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from each population raised on soil to which they were putatively "unadapted" to the growth of the putatively "adapted" type, and the coefficient of selection against the "unadapted" type was estimated as the ratio of the two quantities.

natural selection does little to explain why Jain and Bradshaw tested so many different combinations of parameters. Moreover, given that Bradshaw was already convinced that he had established genuine cases of evolutionary divergence, it is difficult to see why he would have invested as much energy as he did in the project.

Instead, I suggest that Jain and Bradshaw's computer simulation is best understood as an investigative tool, motivated by Bradshaw's attempts to understand the genecological phenomena of evolutionary differentiation and adaptation to environmental conditions in terms of the mechanisms and processes of population genetics. In this light, the computer simulation was a similar undertaking to Bradshaw's broad survey of lead-mine populations: he was motivated not merely to explain the pattern of differentiation that he found on the Goginan mine, but rather to understand the mechanisms responsible for generating those kinds of patterns more generally. Antonovics, who included similar computer simulations in his own dissertation, recalled:

> This was a way to really understand what was going on from the population
> genetics viewpoint. So you could actually go in there, start to see how
> evolution was acting at the level of genes, and ask what the impact of gene
> flow is and how gene flow was balanced out by selection. (Antonovics pers.
> comm.)

Letters between Bradshaw and his post-graduate students at Bangor in 1963 and '64 suggest that his preoccupation at the time was not with shoring up the claim that microgeographic differentiation had occurred, but rather with further characterizing the genetic characteristics of differentiated populations: finding better measures of gene flow and selection intensity, measuring heterozygosity, attempting to artificially select for tolerance in non-tolerant

populations, and carrying out more sophisticated crosses of tolerant and non-tolerant plants to characterize the genetic underpinnings of tolerance itself (D1041/5/2/1/41/1-3). In contrast to descriptive genecological surveys (despite the experimental procedures that he and his students had developed) the computer simulation allowed Bradshaw to manipulate directlythe factors that he considered essential for evolutionary divergence, and explore their consequences.

2.4. Coda

By the time that Bradshaw left Bangor in 1968, he was among the most vocal advocates for the idea that natural selection was constantly and powerfully molding natural populations in ways that could be investigated directly and as they occurred. What began as a genecological survey of pastureland grasses in western Wales—characterizing patterns of heritable variation produced by past evolutionary events—had become a direct investigation of evolution in action. This transformation was not merely a change of mind about the speed of adaptive evolution, but rather a gradual succession of questions, procedures, accidents, and exchanges. In many respects, the move to Liverpool represented a dramatic change of direction for Bradshaw. Instead of a research program primarily oriented toward questions about microgeographic adaptation, Bradshaw reoriented his work toward what became known as restoration ecology. But many of Bradshaw's students continued to work on the problem of local adaptation, and indeed Bradshaw's research on metal tolerance in grasses played a significant role in his contributions to restoration ecology.

CHAPTER 3: PLASTICITY, STABILITY, AND YIELD

A by-product of the variation problem (described in section 1.2.1) is what one might call the *modification problem*. If the variation problem is about distinguishing meaningful contours of organismal variation, the modification problem is about what to do with all of the rest of that variation. In the Linnaean system, variation below the level of the God-given species was merely transient, the "incidental" modification of the species by the pecularities of a given locale—what he called "varieties."

In the 19th century many naturalists, including Darwin, believed in what we would now call the inheritance of acquired characteristics. Variations produced purely by the action of the environment, rather than as a product of heredity, could somehow imprint themselves on the hereditary constitution of an organism and be passed on to that organism's offspring. Darwin's own theory of inheritance, which he called "pangenesis," postulated that somatic changes due to the influence of environment could feed back on the germ, and influence the characteristics of the next generation.

The rise of genetics at the beginning of the 20th century, and especially Johannsen's distinction between the genotype and phenotype, completely reframed the role of individual variations in scientists' understanding of heredity and evolution by separating the hereditary disposition of an organism from its manifest characteristics. Similar to August Weissman's distinction between germ and soma, Johannsen's concept of genotype and phenotype did

not allow for the particular characteristics of an individual organism to exert a causal influence over its hereditary potentialities (Peirson 2012c).

In Chapter 1 I framed Göte Turesson's genecology as a response to the problem of variation. For many later botanists, including Clausen and his team in California, Turesson's genecology was also a response to the problem of modification. In a sense, it was the field botanist's implementation of Johannsen's genotype-phenotype conception. Genecological methods provided a means to distill the hard core of heredity from transient individual characteristics of plants growing in *nature*, not merely the bred strains used by laboratory geneticists. The paring away of environmental modifications in the common garden did not mean, however, that there was no place in Turesson's theory for environmental modification. In fact, Turesson argued—and Gregor and the Carnegie group frequently echoed this idea—that the fact that hereditary differences among ecotypically differentiated populations tended to be in the same direction as environmental modifications was evidence for the claim that such differences were adaptive. In other words, hereditary differentiation and phenotypic responses to the environment were both important aspects of a plant population's adaptation to its habitat.

One of Bradshaw's most influential contributions to the study of evolution in plant populations was to bring the modification problem back into the foreground. In this chapter, I describe the origins of Bradshaw's particular views on the evolution of phenotypic plasticity in plants. Bradshaw's approach to plasticity was shaped in important ways by the particular tradition of genecological research of which he was a part.

3.1. Introduction

In an influential 1965 review in the journal *Advances in Genetics*, plant ecologist Anthony David Bradshaw (1926–2008) suggested that changes in particular traits of individual

organisms in response to specific environmental factors could be under direct genetic

control, and that natural selection could therefore act directly to shape those responses.

> The many different sorts of evidence show unequivocally that the ability of
>
> plants to be modified by the environment is genetically determined. ... This
>
> control is not general to the whole genotype, but is specific for individual
>
> characters, and usually specific for individual environmental influences. ...
>
> Since the degree of plasticity of a character is under genetic control, it must
>
> follow that it can be influenced by natural selection. (Bradshaw 1965)

Thus the idea of "adaptive" phenotypic plasticity—according to Bradshaw, plasticity in a

trait was not merely environmentally induced "noise" obscuring a core genetic signal, but

was potentially specific and refined in the same way as any other adaptive trait.

Although the specifics of its interpretation have changed, Bradshaw's 1965 account

remains a core premise of contemporary models of adaptive phenotypic plasticity in

evolutionary ecology. It sat at the heart of a rapidly expanding and diverse research literature

during the 1980s, as evolutionary ecologists proposed new models for the evolution of

plasticity in a wide range of organisms.[62] The proponents of those models asked questions

like, "How and when is phenotypic plasticity adaptive?", "What is its genetic basis?", "How

might it evolve?", and "How might plasticity impact the direction and dynamics of

evolutionary change?"[63] Those questions continue to drive research at the interface of

ecology and evolutionary biology. Efforts to predict and manage the consequences of

shifting global and regional climates depend on understanding how organisms respond to

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[62] Highly influential works from this period include (among others): Schlichting (1986),
Scheiner (1984), Stearns (1986), Via and Lande (1985), and West-Eberhard (1989).
[63] Nicoglou (2011) addresses the broader history of concepts of plasticity in the life sciences.

changes in their environments. Many scientists are now attempting to integrate the diverse

theories and models of adaptive phenotypic plasticity into predictive models of population

distributions (Chevin et al, 2010; Hoffman & Sgrò, 2011; Reed et al, 2011).

Bradshaw was certainly not the first to call attention to the evolutionary implications of phenotypic plasticity. German limnologist Richard Woltereck intended his experiments on morphological plasticity in Daphnia around 1905, leading to the idea of the "norm of reaction" (now frequently used to characterize plastic responses), to lend support to Darwinian gradualism (Sarkar 1999, Peirson 2012a, 2012b). American geneticist Sewall Wright wrote in 1931 that "individual adaptability is, in fact, distinctly a factor of evolutionary poise," and

Figure 3.1.1. Anthony David Bradshaw (1926–2008). Photograph from press clippings in Bradshaw archive, dated 1972. Bradshaw is shown inspecting a tiller while sitting in grass in an urban setting, presumably in Liverpool. By courtesy of the University of Liverpool Library. D1041/5/1/2/33/2.

"perhaps the chief object of selection" (Wright 1931, p. 147). In the 1940s, Russian

geneticist Theodosius Dobzhansky argued that the evolutionary process leading to higher

cognitive function in humans likely involved selection for plasticity in brain development (Dobzhansky & Montagu 1947). Some Russian biologists did develop theoretical accounts of adaptive phenotypic plasticity in the 1930s and 1940s, but focused mostly on how phenotypic plasticity could alter evolutionary processes, rather than interrogating plasticity in specific traits as products of natural selection (Kirpichnikov 1947, Gause 1947, Schmalhausen 1947, Blacher 1982, Sarkar & Fuller 2003).

The centrality of Bradshaw's ideas to more recent work on adaptive phenotypic plasticity, however, makes understanding the contexts and development of his work in the 1950s and 1960s an important starting-place for contextualizing and analyzing the scientific theories, practices, and discourses that have shaped contemporary models of plasticity.

Along with the surge of interest in adaptive phenotypic plasticity during the 1980s came a new mythology about plasticity research. One example can be found in Schlichting (1986), who wrote that,

> Until 1980, theoretical work on plasticity was limited; and empirical research
> ... was largely unfocused. The reasons for such neglect are puzzling, especially
> considering the clarity of Bradshaw's [1965] review. Surely part of the
> problem was the growing fascination with the detection and measurement of
> 'genetic' variation, of which plasticity must have seemed the antithesis.
> Another problem was that environmentally induced variability in an
> experiment is typically avoided at all costs. Experimental complexity and the
> problem of measuring plastic responses also retarded progress. Thus, only
> recently has phenotypic plasticity become a major focus of experimental and
> theoretical studies. (Schlichting, 1986; p. 669)

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Two elements of that mythology stand out in relation to Bradshaw's work. The first is the impression that, despite occasional insights (especially Bradshaw's), there was little in the way of serious and sustained theoretical or empirical research concerning adaptive phenotypic plasticity prior to the 1980s. The second is the idea that the significance of Bradshaw's model lay in its rejection of a kind of gene-centric myopism—focusing on genetic differences—and its contribution to a "renaissance of the phenotype" (Scharloo, 1989) that emphasized the complex interplay of gene systems and environmental variation.

The main objective of this paper is to enrich our understanding of the context and development of what has become a highly influential understanding of adaptive phenotypic plasticity. In so doing, I hope to dispel some of the mythology described above as it applies to Bradshaw. My central claims are threefold: First, Bradshaw's work on plasticity consisted of a serious and sustained empirical research program in the 1950s and 1960s that went far beyond a single review paper. Second, Bradshaw's investigation was not isolated, but was surrounded by an already rich theoretical discourse and a substantial body of empirical research concerning the evolution of developmental plasticity and stability. Third, Bradshaw's model of plasticity should be seen as a reformulation of that extant discourse—encompassing problems in developmental genetics, population genetics, and plant breeding—within an epistemic framework focused on genetic differences and natural selection. In other words, what made Bradshaw's approach to plasticity different was that he operationalized a concept about the internal relations of whole organisms within an investigative tradition focused on specific adaptive traits and specific environmental factors.

In section 2, I provide an overview of Bradshaw's training in the agro-ecological tradition of genecology, and his ideas about intraspecific evolution in plants. In section 3, I describe some of Bradshaw's early ideas about phenotypic plasticity, his exchanges with

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population geneticist John M. Thoday, and his earliest experiments concerning plasticity in *Agrostis tenuis* (browntop, a.k.a. colonial bent grass). In section 4, I focus on Bradshaw's experiments with barley in 1963 and 1964 at the University of California, Davis, where he spent a sabbatical year working with population geneticist Robert Wayne Allard (1919–2003). It was during that collaboration that Bradshaw's ideas about plasticity crystalized. In section 5, I briefly summarize the content and direction of Bradshaw's research on plasticity following the Davis sabbatical.

<div align="center">3.2. The Genecological Approach</div>

Bradshaw began his training as a genecologist at the Welsh Plant Breeding Station (WPBS), in Aberystwyth, in 1948. He continued his dissertation research after taking a position in 1950 as Assistant Lecturer in the Department of Agricultural Botany at the University College of North Wales, in Bangor, and eventually completed his dissertation in 1959. In this section, I introduce genecology as an agricultural research tradition in Britain, and provide an overview of Bradshaw's early investigations of infraspecific evolution in plant populations. By the late 1950s, Bradshaw advocated a model of evolution in plant populations in which strong natural selection and attenuated gene flow produced a "graded patchwork" of local adaptation on very short time-scales. Bradshaw's genecological training and his ideas about local evolution provided the epistemic backdrop for his account of adaptive phenotypic plasticity in the 1960s.

Genecology, also known as "experimental taxonomy" or (later) "biosystematics," emerged in the first decades of the 20th century as a heterogeneous and interdisciplinary mix of biogeography, cytology, genetics, and field botany (Hagen, 1984, 1986; Kleinman, 2009). In the 1910s and 1920s, botanists in Europe (Turesson, 1922a, 1922b), Russia (Sinskaja, 1931), the United States (Clements, 1908, 1929; Clements & Hall, 1919), and Britain

(Stapledon, 1913, 1928; Summerhayes & Turrill, 1939; Gregor & Sansome, 1927; Gregor, 1931, 1938) advocated an experimental approach to the study of genetic variation within plant species. Some genecological research was framed as a more holistic approach to addressing taxonomic questions at or below the level of the species, in contrast to reliance on morphological studies of museum or herbarium collections (Hagen, 1984, 1986). A great deal of genecological research, however, had a far more practical orientation: understanding the patterns and causes of genetic variation among plant populations, and leveraging those differences to improve agricultural production.

The linkage between genecology and agriculture in Britain has deep roots. The WPBS was established in 1919 by Reginald George Stapledon (1882–1960) with funding from steel and shipping magnate Lord Milford, and later from the Ministry of Agriculture and the Empire Marketing Board (Palladino, 2002; Ellis, 1972; Moore-Colyer, 1982). Prior to and during the first world war, an abundance of cheap feed for stock shifted land-use priorities away from maintaining grazable pasture-land and toward crop production (Moore-Colyer, 1982). As the war drew to a close, however, the long-term problem of providing sustainable sources of protein for a growing British population raised concerns about food security: the continued ability to import cheap feed was not guaranteed, raising the question of how to re-establish productive pastures in Britain (Moore-Colyer, 1982). Stapledon was vocal about the importance of converting "derelict" upland areas to rotational "ley" farming, and of developing varieties of grasses and other herbage plants that could maintain high productivity on exposed and infertile hilltops. Demonstration projects,[64] grassland surveys,[65]

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[64] E.g. the Cahn Hill Improvement Scheme, a privately funded large-scale farm trial that focused on grasses, clovers, and rapeseed.

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and an escalating rhetoric of war-time food security during the 1930s galvanized an argument for the 'ploughing-up' of British hill-sides.

The cornerstone of Stapledon's paradigm for plant breeding at the WPBS, based on his research on *Dactylis glomerata* (cock's-foot grass) in the 1910s (Stapledon, 1913, 1928), was sourcing material from local populations that were adapted to prevailing conditions of soil, climate, and grazing. Stapledon and Thomas James Jenkin (1885–1965)[66] argued that improvements in the long-term productivity of pasturelands required "making the habitat as suitable as possible to the desirable indigenous species," and by "establishing local supplies of ... indigenous seed" (Stapledon & Jenkin, 1916, p.62).

Stapledon's ideas about locally-adapted populations ran parallel to Swedish botanist Göte Turesson's (1892–1970) account of intraspecific varieties, or "ecotypes," and Stapledon readily adopted Turesson's terminology (Stapledon, 1928). Turesson described ecotypes as "the genotypical response of an ecospecies to a particular habitat," produced by natural selection (Turesson, 1922a). By "genotypical response," Turesson meant that selective pressures exerted by particular habitats would act to filter standing genetic variation within a species, producing hereditarily distinct habitat-specific ecotypes. According to Turesson, the genecologist's task was to detect and describe patterns of ecotypic differentiation using experimental methods designed to suppress phenotypic plasticity (Turesson, 1922a, 1922b, 1923, 1925).

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[65] E.g. William Davies' recent country-wide pastureland survey, commissioned by the Ministry of Agriculture in 1938.

[66] Jenkin was an Honours student in botany at UCW, who would become Stapledon's long-time research partner and eventual director of the WPBS (Moore-Colyer 1982).

The genecological approach involved two principle experimental methods. The "common garden" technique involved collecting individual plants (either as seed, or as vegetative cuttings) from contrasting habitats, and growing them under uniform conditions. Common garden experiments minimized phenotypic differences due to environmental variation, so that any remaining differences among samples could be attributed to heredity. A similar "reciprocal transplant" method was developed by Frederic E. Clements and Harvey M. Hall at the Carnegie Institution of Washington in the 1910s, and was popularized by Jens Clausen, David Keck, and William Heisey in the 1930s and 1940s (Hagen, 1982; Smocovitis, 1988). Those experiments involved collecting plants from contrasting environments, and growing them at each of a series of stations spread from the Stanford University campus (100 feet above sea level) to a site known as "Timberline" (around 10,000 feet), beyond the ridge of the Sierra Nevada mountain range. Ecotypes that were indistinguishable in one environment would often exhibit dramatic differences when grown in a contrasting environment, due to phenotypic plasticity.

As concerns about long-term food security in Britain mounted prior to and during the second world war, genecologists continued to hunt for ecotypes that could improve the grazing potential of marginal, derelict, and upland pastures (Moore-Colyer, 1982). Genecologists sampled populations of forage grasses, clovers, and other herbage plants throughout Britain and western Europe, and tested those plants in carefully controlled experimental plots in order to find hereditary differences that could be further developed through breeding (e.g. Beddows, 1949).

When Bradshaw arrived at the WPBS in 1948, the application of genecological methods to agricultural improvement remained a dominant part of the station's research agenda. Bradshaw recalled that, "the heritage of George Stapledon was never far away"

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(D1041/13/2/9). The genecological approach had uptake not only at the WPBS, but also by James Wylie Gregor (1900–1980) at the Scottish Plant Breeding Station (SPBS), near Edinburgh, starting in the 1920s (Gregor & Sansom, 1927). Gregor was among Bradshaw's most influential mentors during the early stages of his career (D1041/13/2/9).[67]

Bradshaw's dissertation research at the WPBS focused on the genecology of *Agrostis tenuis* (colonial bentgrass) and *Anthoxanthum odoratum* (sweet vernal grass). Both species had potential for use on acidic soils and exposed upland grazings (Davies, 1952, 1953; Jones, 1956; Beddows, 1956).[68] Bradshaw conducted a broad genecological survey in western Wales and southern England, using both common garden and reciprocal transplant methods. Bradshaw spent much of the 1950s building a research program around populations of heavy-metal tolerant *Agrostis* that he found during his initial survey (first reported in Bradshaw, 1952). Bradshaw hypothesized that particular populations of Agrostis were specially adapted to specific heavy metals, and that those adaptations were the result of powerful and ongoing natural selection at the edges of abandoned mineworks. That hypothesis prompted a multi-pronged research program involving further genecological trials, physiological experiments, field studies of seed and pollen dispersal, and (in the 1960s)

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[67] The link between genecology and agricultural research had significant consequences for international agricultural policy, as described by Pistorius (1997). Gregor, and his students and collaborators, played a significant role in translating genecological methods and theory into international policy, in part via their involvement with the United Nations Food and Agriculture Organization.

[68] Research on *Agrostis* for breeding purposes started in the early 1920s (NLW E25/6), and showed up again in the 1940s (NLW E37/13–14; NLW C5/1). Arthur Rhys Beddows, head of the grass breeding department at the Welsh Plant Breeding Station, hailed Bradshaw's genecological research as a contribution to the grass breeding program. "We have in addition two new strains, one of bent grass (*Agrostis tenuis*) and the other of sweet vernal grass (Anthoxanthum odoratum), both of which may be more useful in the less fertile marginal areas" (Beddow, 1956, p.13).

computer simulations (Bradshaw *et al.,* 1958, 1960a, 1960b, 1964; Bradshaw & Snaydon, 1959; Bradshaw, 1963, 1966; Gregory & Bradshaw 1965; Aston & Bradshaw 1966; Jain & Bradshaw, 1966).

Genecologists at the WPBS and SPBS differed from other genecologists, both in Britain and abroad, in the way that they conceptualized ecotypes. As early as the 1940s, there was growing disagreement about what counted as evidence for distinct ecotypes, and about the evolutionary and taxonomic relationships between ecotypes and other intra- and intraspecific units (e.g. see Bennett, 1964). Although Gregor had previously advocated a genecological systematics in parallel to traditional taxonomy (Gregor, 1931; Gregor *et al.,* 1936), by the 1940s he and his collaborators had moved away from attempts to diagnose ecotypes as distinct, coherent, and namable entities. Instead, they focused on detecting and explaining ecotypic differentiation in *individual characters* as adaptations to *specific environmental factors*. SPBS staffer Frederick Earnshaw summarized this approach in a session on experimental taxonomy at the 7th International Botanical Congress in Stockholm, Sweden, in 1950:

> Gregor has emphasized that each population must be influenced by a
> complex of environmental factors, each capable of independent variation. He
> therefore considers it will be preferable to trace eco-clinal variation in
> response to particular ecological gradients, rather than to attempt to name
> local populations as distinct ecotypes. (Earnshaw, 1950)

The rejection of discrete, objectively-delimitable ecotypes entailed a strongly operational view of the ecotype concept. When Gregor, Bradshaw, and their colleagues talked about "ecotypes," "clines," or "demes," they referred to patterns that they observed and stabilized

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using genecological methods, and *not* to natural kinds or entities that exited independently of those observations (Bradshaw, 1962).[69]

That emphasis on linking variation in specific traits to variation in specific environmental factors was a crucial component of Bradshaw's epistemic framework. Like

Figure 3.2.1. Survivorship in samples of *Anthoxanthum odoratum* during a very severe drought in 1949 was correlated with the mean annual rainfall at the sites where they were collected. Bradshaw's unpublished figure is shown at right (D1041/2/8/1). By courtesy of the University of Liverpool Library. Data replotted at left.

many of his peers, Bradshaw recognized that there were complex developmental linkages

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[69] This shift in emphasis, and a growing body of evidence from the field, suggested that evolution could occur rapidly and locally enough to be observed "as it occurred," and not merely in retrospect.

among traits, and that those linkages could impact evolutionary processes. But when it came

to making claims about ecotypic differentiation, the kind of evidence that mattered was

strong geo-spatial correlations between specific phenotypic traits and specific environmental
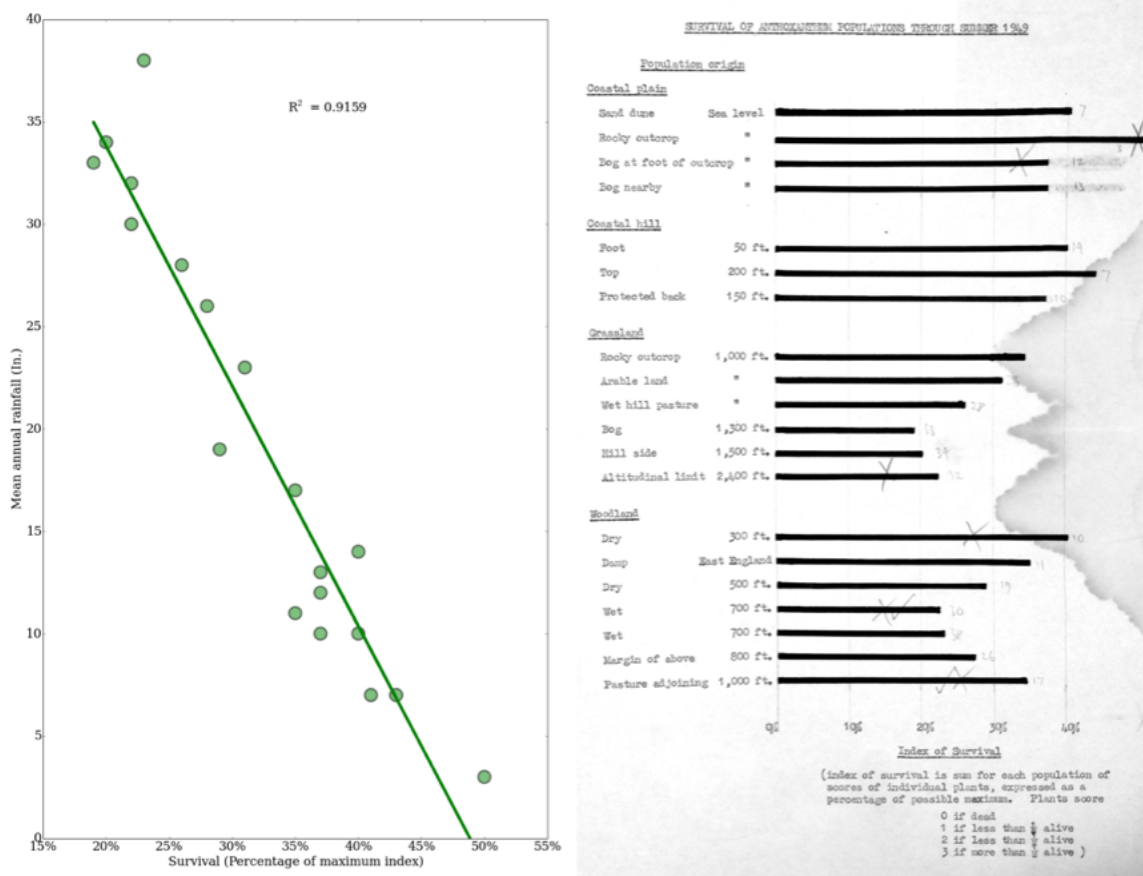
factors. For example, Bradshaw found that differences in survivorship in samples of

Anthoxanthum odoratum during a very severe drought in 1949 were closely correlated with

mean annual rainfall at the sites where they were collected (Figure 3.2.1).

Bradshaw's epistemic commitments, described above, were tied to a model of

intraspecific phenotypic evolution in which the spatial distribution of a species, the "pattern

of the environment," and the availability of genetic variation played dominant roles. Over

the course of the 1950s Bradshaw was increasingly vocal in asserting that, even in wind-

pollinated outbreeding plants like *Agrostis*, gene flow was often sufficiently attenuated and

natural selection sufficiently strong to cause differentiation over distances of 100, 50, or even

15 meters.[70] "As a result," Bradshaw wrote, "population differentiation could occur in

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[70] Bradshaw (1952) reports differentiation over 100 yards, and in Bradshaw (1959 I.) that
number drops to 50 meters. McNeilly and Bradshaw (1968) report differentiation over a
distance of 15.5 meters. Bradshaw's ideas about microgeographic adaptation in plants, and
its consequences for interpreting and classifying so-called 'ecotypic differences,' ran
counter to the views of prominent genecologists and other evolutionary biologists in the
United States, including the notorious and influential 'Carnegie trio' of Jens Clausen,
William Hiesey, and David Keck at the Carnegie Institute of Washington in Stanford,
California (Clausen *et al.*, 1939, 1940, 1947, 1948). On a visit to the Welsh Plant Breeding
Station, Keck dismissed Bradshaw's findings as "accidents" (D1041/13/2/9). After
Bradshaw published the results of his genecological survey in the late 1950s, Clausen wrote
to Bradshaw that "As far as I can see, the area that has been sampled is climatically so
uniform that no climatic ecotypes should be expected to exist ... It may come as a surprise
to you, but I have a suspicion that the major part of the island of Great Britain probably
belongs to one climatic zone." (D1041/5/1/1/17).

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relation to very local variations in environment. The data[71] show exactly this" (Bradshaw, 1959, p.223).

By the end of the 1950s, Bradshaw saw plant populations as a "graded patchwork" of morphological and physiological adaptations to extremely local environments (Bradshaw, 1959, 1960).

> It is the environment, even its local variations, which determines the pattern
>
> of the differentiation [in plant populations]. So where there are sharp changes
>
> in environment, e.g. from the foot to the top of Pen Dinas, there are sharp
>
> correlated changes in the populations.[72] Where there are gradual changes in
>
> environment, e.g. from the foot of Pen Dinas to the summit of Plynlymon,
>
> the population changes are equally gradual.[73] Where in such gradients there
>
> are sudden local variations, e.g. Goginan mine, there are sudden population
>
> changes.[74] (Bradshaw, 1959, p.224)

Following Gregor, Bradshaw dismissed attempts to classify plant populations as distinct ecotypes as "subjective," and considered any system of infraspecific taxonomic classification to be "a source of confusion" (Bradshaw, 1959, p. 225). Bradshaw saw natural selection as

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[71] Bradshaw refers to his genecological survey of *Agrostis tenuis*.

[72] Pen Dinas is a hill to the south of Aberystwyth. The top of the hill is exposed to strong sea winds from St.George's Channel, whereas the pasture at the foot of the hill is very effectively sheltered by the surrounding topography. Bradshaw found that *Agrostis* at the top of the hill have evolved to have a 'dwarf' stature and low yield, spreading primarily through protected subterranean stolons. *Agrostis* at the foot of the hill were taller in stature, with higher yield.

[73] Plynlymon is the highest hill in Wales, at 2,468 feet. The gradient mentioned here is the transition from low to high altitude, accompanied by a shift from arable *Agrostis-Festuca* and *Lolium-Agrostis* pastures to the *Nardus*-dominated exposed upland grazings.

[74] Bradshaw found a population of heavy-metal tolerant *Agrostis* growing on a contaminated tip at Goginan mine in the early 1950s. The *Agrostis* surrounding the mine was non-tolerant, despite being almost directly adjacent to the tolerant plants.

the foremost explanation for patterns of differentiation in plants, writing that, "All explanations ... must be considered but in most cases it is unnecessary to postulate the effects of anything other than natural selection" (Bradshaw, 1959, p.225).

Bradshaw also saw local adaptive evolution as a potentially rapid process. When he began his research in 1948, Bradshaw thought that even six thousand years was insufficient for plant populations to become adapted to changes in their environments (D1041/1/11/87). But by the 1960s Bradshaw's understanding of the speed of adaptive evolution had dramatically changed. "We are brought up to think that the time scale of evolution is millennia," he wrote; "This may be true for the history of life but it is not true for the immediate process of evolution within species." (Gregory & Bradshaw, 1965). In a presentation to the British Ecological Society in 1968, Bradshaw asserted that "even twenty five years grossly over estimates the time needed" for the evolution of particular phenotypic traits (D1041/1/11). Bradshaw's change of mind is representative of a broader shift in thinking by ecologists about the temporal and spatial scales of evolutionary change during this period that merits further investigation (Collins, 1986).

3.3. Early Experiments: Phenotypic Flexibility in *Agrostis*

"There seem to be so many facets of [phenotypic plasticity] that it is difficult

to know exactly what terms to use and almost where to begin." (Letter from

Bradshaw to Ken Lewis, Oxford Botany School, March, 1961;

D1041/4/3/21)

In the last section, I introduced the main epistemic context for Bradshaw's early research, a particular flavor of genecology practiced at the Welsh and Scottish Plant Breeding Stations. In this section I describe Bradshaw's early ideas about adaptive phenotypic plasticity, and a

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series of unpublished experiments that explored those ideas. Bradshaw's earliest notes and correspondence on this topic place his ideas in the context of a broader discourse surrounding the relationship between heterozygosity and developmental stability, and highlight some of the tensions that motivated his work on plasticity in the 1960s.

3.3.1. A nagging observation

By the mid-1950s, Bradshaw was wrestling with a nagging observation. In many cases, the differences that he found between *Agrostis* populations in his carefully-controlled common garden experiments were less distinct than what he had observed in the field (D1041/13/2/9). If, for example, plants from one population grew taller and more densely than another population in the common garden, then that difference tended to be far more pronounced—perhaps twice or three times so—in the field. Bradshaw inferred that that (phenotypic) responses to the environment during development were very important component of (genetic) adaptation to specific environments.

In the fall of 1957, Bradshaw began to articulate his ideas about plasticity. On 23 November, Bradshaw floated those ideas in a presentation to the Genetical Society of Great Britain at the University College, London. Bradshaw noted that some closely related species, and perhaps even populations within a single species, differ in their "phenotypic flexibility" (Bradshaw, 1958). Certain species of *Potamogeton* (pondweed), for example, develop floating leaves just at the water's surface, while others do not (D1041/4/3/29). Likewise, the leaves of *Ranunculus* subgenus *Batrachium* (the water buttercup, or water crowfoot) develop markedly different forms depending on whether the plant is submerged, and that response differs greatly among species within the subgenus (D1041/4/3/28). Bradshaw argued that, "phenotypic flexibility must ... be a character with an ordinary genetic basis," and that "its

occurrence in species and in populations will be under the control of the normal processes of natural selection" (Bradshaw, 1958).

During the ensuing discussion, Bradshaw's presentation drew a rude[75] rebuff from geneticist John Marion Thoday (1916—2008) (D1041/4/3/27/8). In a paper at the Society for Experimental Biology's symposium on Evolution in 1952, Thoday discussed phenotypic flexibility as part of a larger theoretical account of fitness and "evolutionary progress" (Thoday, 1953), and Bradshaw's conceptualization of flexibility seemed dissonant. The confrontation led to an exchange of letters a few weeks later, in which Thoday and Bradshaw staked out their positions more clearly.

Thoday agreed with Bradshaw about the adaptive significance of phenotypic flexibility. But whereas Bradshaw defined flexibility as "the ability of a genotype to vary its expression in different environments," (D1041/4/3/27/8) Thoday defined phenotypic flexibility as the capability of an organism "of adapting itself to varying external conditions so that ... it *maintains* its characteristics" (Thoday, 1953, p. 99; emphasis added). Thoday thought that Bradshaw's emphasis on morphological differences entailed too narrow a conception of the phenotype, which ought also to include biochemical and physiological characteristics. Bradshaw, on the other hand, thought that Thoday's account was inappropriate for plants. Bradshaw wrote to Thoday,

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[75] Bradshaw characterized Thoday's comments as rude (D1041/4/3/27/8), although the frankness of their exchange may have been due in part to an underlying friendship. Their correspondence shows that they were already on a first-name basis. This would not be surprising since Thoday's father, David Thoday (1883–1964), occupied the chair of Botany at UCNW Bangor until 1949, and Bradshaw and the Thodays surely had many social and professional ties in common.

The confusion stems, as far as I can see, from the difference between the

animal and the plant approach. I can understand how your concept fits

animals well, since a phenotype which can exist in different environments

without change could well be said to be flexible. But in plants the position is

rather different. Many are able to exist in several different environments only

as a result of considerable phenotypic changes. This is where the use of the

term phenotypic flexibility gets a bit difficult. (D1041/4/3/27/8)

In response, Thoday suggested that Bradshaw adopt taxonomist William Bertram Turrill's

(1890–1961) concept of "plasticity:" the kind of measurable environmentally-induced

phenotypic variation that the genecologists' common-garden cultivation experiments were

designed to minimize.

Bradshaw agreed, noting that, "I will have to make it quite clear that there are two

sorts [of plasticity], that which is adaptive and that which is not" (D1041/4/3/27/8).

Bradshaw thus faced the problem of discriminating between adaptive and non-

adaptive plasticity. He wrote to Thoday,

I want to go on from your deliberations in S.E.B. Symposium 7 and consider

the actual types of habitats in which phenotypic flexibility is likely to be

important, and the plants with high plasticity which substantiate this.

(D1041/4/3/27/8)

The crux of Bradshaw's struggle with Thoday's account of phenotypic flexibility at that time,

however, was that it gave little guidance about what kinds of phenotypic changes were

adaptive and which were not. Thoday conceded that,

When it is approached from the end of observation we are in difficulties

because it is clear that observable variation of phenotype with variation of

environment may be evidence for adaptive changes, but may equally well be

evidence that the particular genotype we are studying has no phenotypic

flexibility and gets pushed around in undesirable ways by the environmental

conditions. (D1041/4/3/27/6)

For a genecologist interested in the adaptive relationship between individual characters and

specific environmental factors, the lack of a clear empirical criterion in Thoday's

conceptualization of phenotypic flexibility was a grave deficiency indeed.

3.3.2. Bradshaw's First Experiments

Bradshaw was not deterred by Thoday's reaction to his presentation at the Genetical

Society, and mapped out a series of eight experiments to be carried out in the summers of

1958 and 1959. Those experiments would examine differences in plasticity among

populations of *A. tenuis* and *stolonifera*, and among regional varieties of *Polypogon*, *Dactylis*

glomerata, Sonchus oleraceus (sow thistle), and *Hypercium perforatum* (St. John's wort), in response

to soil moisture, fertility, and grazing.

Bradshaw approached the problem of discriminating between adaptive and

nonadaptive plasticity as a genecological one. In his research notes, Bradshaw wrote:

The normal pattern of evolution is such that characters are only developed to

any marked extent in those situations where they are adaptive. In situations

where they are neutral they are lost slowly or very slowly; where they are

nonadaptive they are usually lost quickly unless other factors are operating.

Bearing this in mind it should be possible to indicate situations in which

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plasticity is distinctly advantageous and discover examples to substantiate this.

Just as a strong correlation between a particular environmental factor and hereditary variation in a trait would count as evidence for adaptive (ecotypic) differentiation, so to would a correlation between environment and a plastic response.
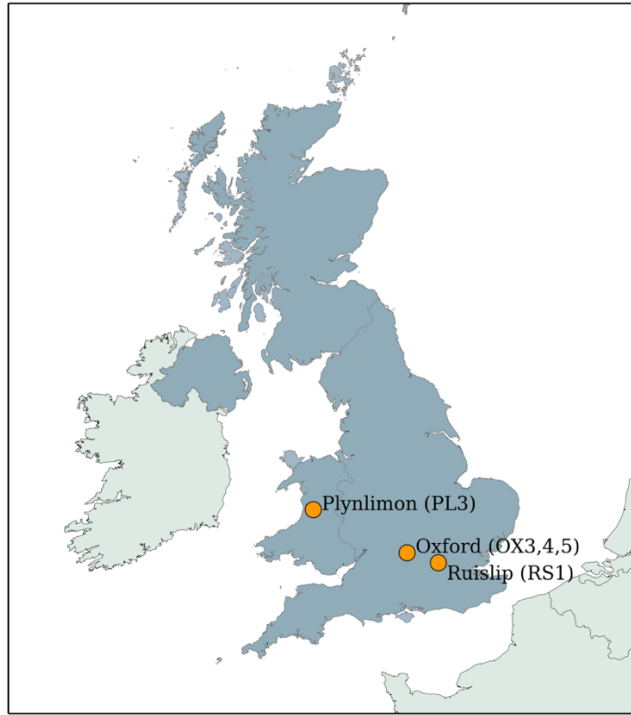
Figure 3.3.1. Collection sites for Bradshaw's experiments on phenotypic plasticity in Agrostis in 1958 and 1959.

Bradshaw carried out his first experiments on phenotypic plasticity in *Agrostis* in the spring and summer of 1958, focusing on responses to both soil moisture and fertility.[76] He collected tillers (side-shoots) of *Agrostis* from five sites among the thirty-three in his original genecological survey (Figure 3.3.1):

1. PL3: *A. tenuis* from the exposed, infertile top of Plynlymon, near Bangor. Shorter plants with a dense growth habit and lower yield, relying almost entirely on subterranean rhizomes (rather than exposed stolons) to spread.

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[76] Bradshaw's notes indicate that he carried out a third experiment, with *Polypogon monspeliensis*, in 1959. But no data from that experiment remain among his papers.

2. RS1: *A. tenuis* from a more fertile "damp oakwood on acid clay" (Bradshaw, 1959, p. 214) at Ruislip, northwest of London. Taller plants with more lateral growth and higher yield, spreading almost entirely by stolon.

3. OX5: *A. tenuis* from a heavily grazed lowland meadow near Oxford, preferring "drier areas poor in bases" (Bradshaw, 1958b, p.81). A taller plant with less lateral growth, and lower yield.

4. OX3: *A. stolonifera* from the same site as OX5, preferring wetter areas. Shorter than OX5, but with much higher yield and more lateral stoloniferous growth.

5. OX4: Apparent hybrids of OX5 and OX3, that "combine the ability to spread of *A. stolonifera* with the high density of tillers of *A. tenuis*" (Bradshaw, 1958b, p. 77). Bradshaw found these hybrids interesting because they occurred under conditions intermediate to those preferred by their parents, and exhibited intermediate phenotypes.[77]

Bradshaw chose those populations (1) to represent widely contrasting habitats (e.g. RS1 vs PL3), and (2) to explore the idea that the presence of OX4 hybrids was explained by the availability of conditions intermediate to those preferred by *A. tenuis* and *A. stolonifera*.

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[77] Bradshaw had found other such hybrids at ecologically similar sites around southern England. In his discussion of the *A. tenuis* x *A. stolonifera* hybrids, Bradshaw referred to Edgar Anderson's concept of "hybridization of the habitat," in which environments intermediate to those preferred by two closely related species provide opportunities for the emergence and establishment of hybrids.

Bradshaw planted tillers three-to-a-pot in a corner of the greenhouse, and arranged them into six replicates of four treatments: low fertility dry, low fertility wet, high fertility dry, and high fertility wet. After the plants established themselves in their pots, he cut them back to 1/2" above the soil surface, and began watering the plants in the wet and dry treatments discriminately. Four weeks later he supplemented the high-fertility pots with John
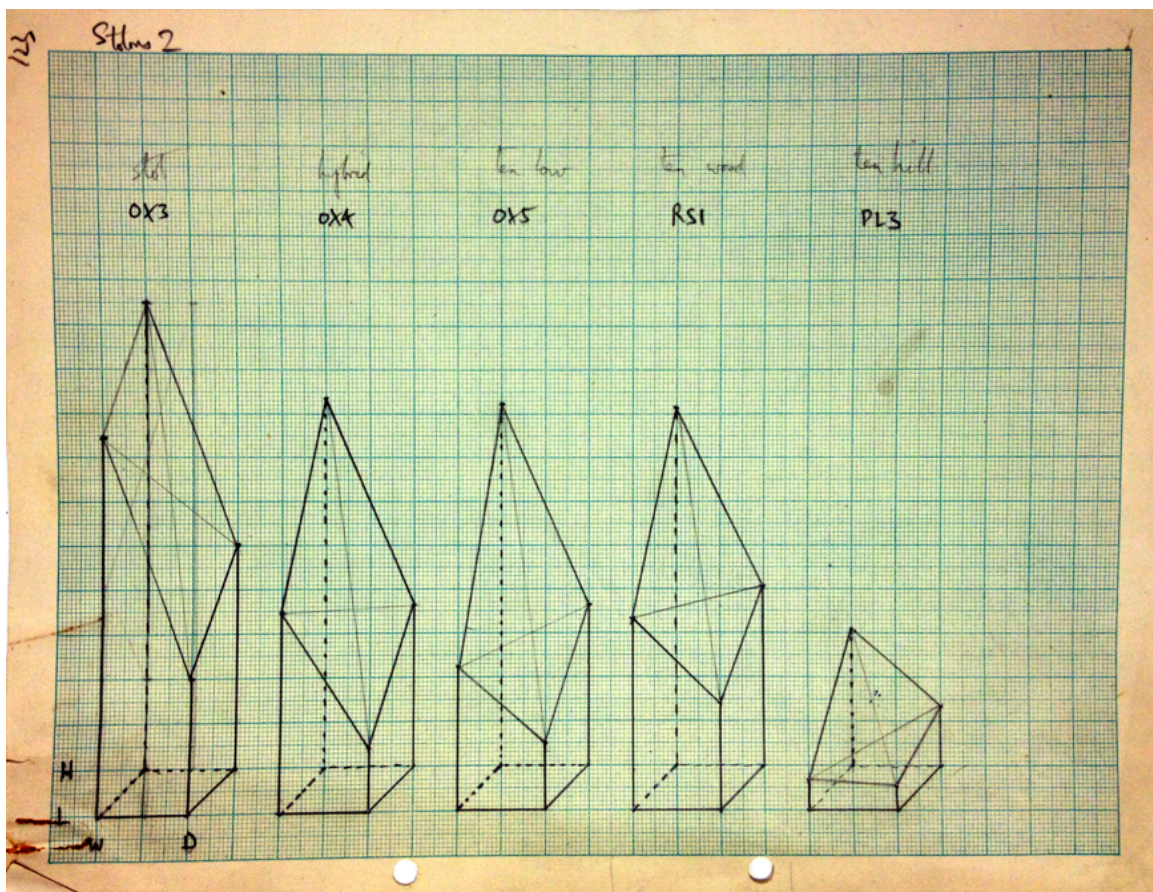
Figure 3.3.2. Hand-drawn figure by Bradshaw depicting population differences in stolon length in response to soil moisture and fertility. By courtesy of the University of Liverpool Library. D1041/4/3/23.

Innes "L" Feed.[78] Seven weeks after the fertilizer treatment he cut the plants back again, and measured four traits for each plant: dry weight, stolon length, overall above-ground plant length, and number of tillers. For each trait, he used an analysis of variance (ANOVA) to

Figure 3.3.3. Differences in response to soil moisture and fertility among plants collected from five populations of *Agrostis* spp. Data for the experiment ending 22 August, 1958, as recorded in Bradshaw's notebooks.

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[78] 18 parts N, 6 parts P_2O_5, and 6 parts K_2O.

test for differences between populations in their response to soil moisture and fertility (D1041/4/3/23/4).

The experiment yielded dramatic differences between populations in their response to varying soil moisture and fertility, except in dry weight. Brad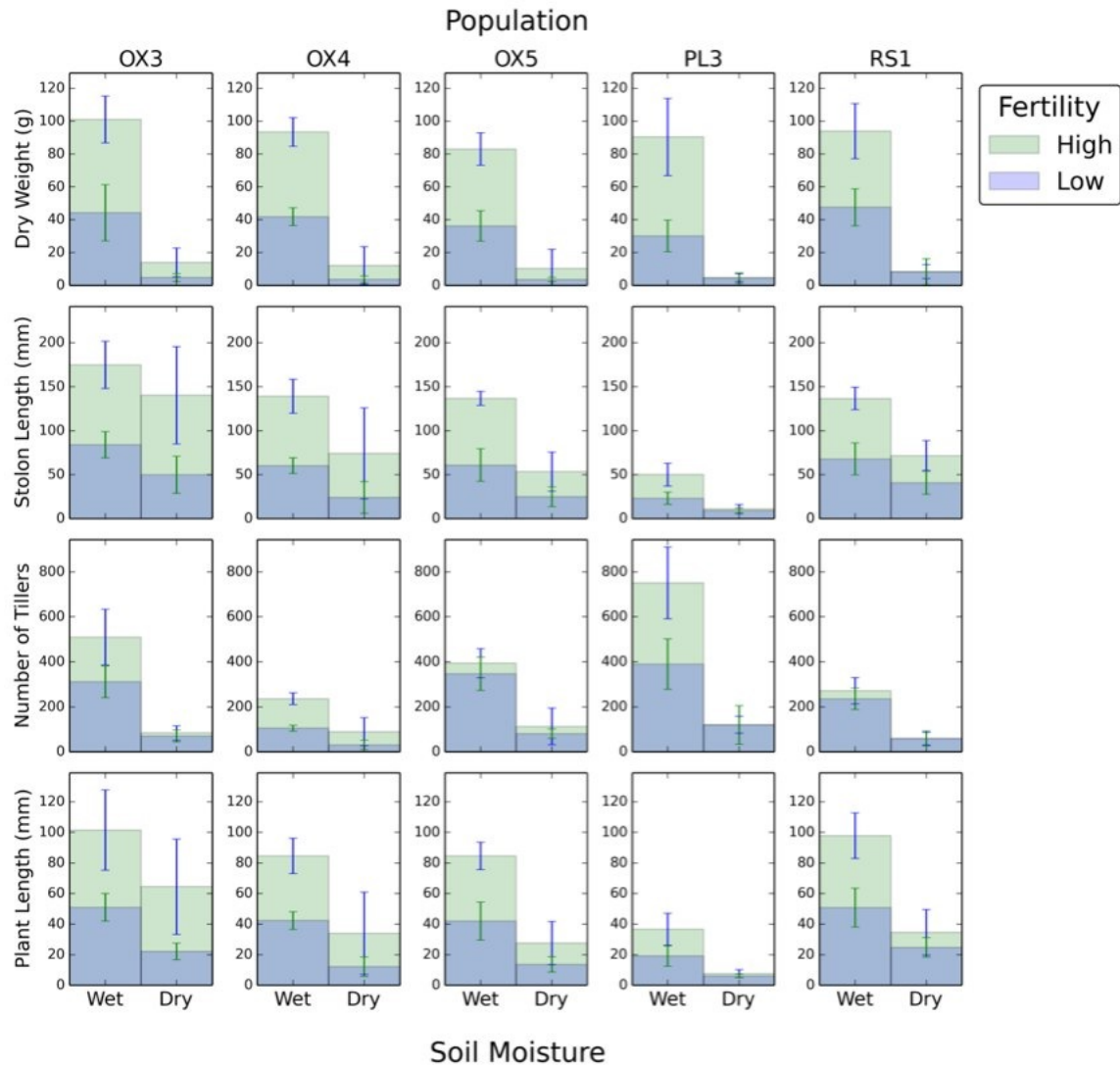shaw repeated the whole procedure twice, and some of the results from the second harvest are shown in figure 4. The four populations of *Agrostis* varied in their response to soil moisture in stolon length, overall plant length, and number of tillers. The differences among populations in response to soil fertility were somewhat less dramatic, with differences only in plant length and number of tillers.

Bradshaw conducted a set of follow-up experiments in the summer of 1959. This time he focused only on response to soil moisture, and excluded the hybrid population from Oxford (OX4). This allowed him to increase both the number of replicates and the number of plants per replicate, and to repeat the experiment in both outdoor garden plots (planting in May, harvesting in July) and in boxed beds in the greenhouse (planting in July, harvesting in October). The results were consistent with those from the 1958 experiment (Figures 3.3.3 and 3.3.4).

Although Bradshaw's work on plasticity tapered somewhat after the summer of 1959, he remained "rather stuck on the subject" (D1041/4/3/21). In the autumn of 1960 he wrote to the director of the Institute of Plant Systematics and Genetics at the Royal Agricultural College in Uppsalla, asking for samples of two varieties of *Polygonum amphibium*
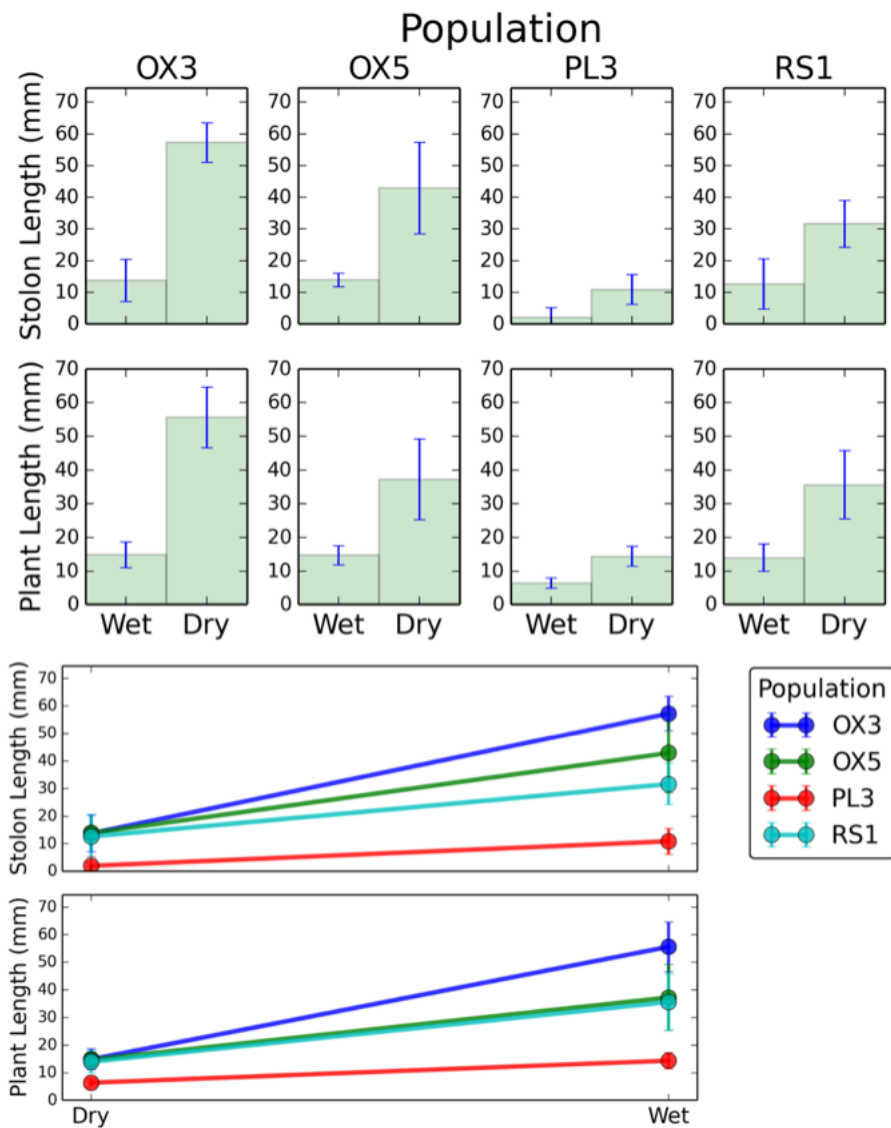

Figure 3.3.4. Differences in response to soil moisture among plants collected from four populations of *Agrostis tenuis*. Tillers sampled from each population were planted on 13 May, 1959, in spaced plots outdoors. Data from Bradshaw's notebooks.

(water knotweed) that Turesson had shown him a decade prior: one of which was highly plastic, and the other of which was not (D1041/4/3/20).[79] It does not appear that he ever received that material, despite repeated requests. But those attempts are evidence of a sustained effort to approach the phenomenon of plasticity experimentally and comparatively.

3.4. The Barley Experiment at Davis

Meanwhile, many changes were afoot at Bangor, some of which conspired to reorient Bradshaw's research on plasticity and pave the way for a collaboration with population geneticist Robert W. Allard at Davis. After a two-year search, Oxford-trained ecologist John Lander Harper replaced R. Alun Roberts as Professor of Agricultural Botany at Bangor.[80] Before coming to Bangor, Harper spent a year at the University of California, Davis, working with the chair of the newly-established Department of Genetics, George Ledyard Stebbins (1906–2000). Between the buzz surrounding Bradshaw's research group on mineral nutrition and heavy metal tolerance, and Harper's own burgeoning acclaim and connections to botanists in the United States, Bangor was becoming a "mecca" for plant ecologists.

Harper's connection to Davis botanists likely helped to pave the way for Bradshaw's collaboration with Allard in 1963 and 1964. While at Davis, Harper advised Allard on an experiment concerning the stability and yield of genetically diverse strains of lima bean

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[79] Knotweed is known for its two distinct environmentally-induced growth forms—terrestrial and aquatic—that differ greatly in leaf shape and overall growth habit. In 1950 Bradshaw had attended the Botanical Congress in Stockholm and, while on a tour of the botanical garden at Uppsala, Göte Turesson showed Bradshaw two varieties: one which responded to environmental conditions, and one which did not.

[80] Bradshaw had applied for the post in 1958, with support from Roberts, tropical ecologist Paul Richards, and Herbert Baker. The search committee was unusually vague in their official reports to the College Council during this process, so it is unclear who else applied for the post. Perhaps Bradshaw's aspiration toward a full Professorship was premature: after all, Bradshaw had yet to actually acquire his Ph.D., despite a portfolio of almost twenty research publications. Harper accepted the position prior to his sabbatical in 1959.

(Allard 1961). In 1961, Stebbins visited Harper at Bangor. Bradshaw was drafting a manuscript about the conceptual issues surrounding phenotypic plasticity (D1041/4/3/21), and discussed his ideas with Stebbins (D1041/4/3/19). Soon, a plan was hatched for Bradshaw to visit Davis and work with Allard on the problem of the genetic and adaptive basis of plasticity and stability.

Finally, in 1963, Bradshaw secured a research fellowship from the Leverhulme Trust to fund the long-awaited trip to Davis. That autumn, after moving himself, his wife, and his two daughters "across the pond," Bradshaw began an extensive experiment concerning phenotypic plasticity in barley. Prior to his departure, Bradshaw coordinated with Roger Whitehouse at the Plant Breeding Institute, in Cambridge, to establish a set of parallel experiments at Bangor in his absence. Those experiments would involve a few varieties of barley and of two species of oat: bred varieties of *Avena sativa*, the modern cultivated cereal, and the wild oat *Avena strigosa*. Bradshaw also tasked a new Ph.D. student, Muhammed Akram Khan (an aspiring plant breeder from Pakistan), with studying plastic responses to density in flax.

Table 1. Twelve varieties of barley in Bradshaw's experiment at Davis, 1963–1964.				
	Adapted	Unadapted	Stable	Unstable
Arivat	✔		✔	
Atlas	✔		✔	
Club Mariout	✔		✔	
California Mariout	✔		✔	
Vaughn	✔			✔
Rojo	✔			✔
Trebi		✔	✔	
Traill		✔		?
Firlbecks III (2 row)		✔		?
Abyss Irregular		(✔)		?
Abyss, 6 row: CI 1227		(✔)		
Abyss, 2 row: CI 2376		(✔)		
Transcribed from Bradshaw's notebooks (D1041/2/15).				

Bradshaw's experiment at Davis sat at the intersection of multiple scientific and agroeconomic contexts that were crucial for his 1965 account of adaptive phenotypic plasticity. Unfortunately, Bradshaw never published the results of that experiment, and only a small fragment of the data remains in his archive. Some indications of the results can be found in subsequent correspondence and grant applications. Yet ultimately it is the *design* of Bradshaw's experiment, rather than its results, that provide the most telling indications of the driving questions and contexts for his account of adaptive plasticity.

The barley experiment was relatively simple, albeit large. In mid-November, 1963, Bradshaw selected twelve varieties of barley (*Hordeum vulgare*), seven of which were well-adapted to the Mediterranean climate of north-central California (Table 1). Of the adapted varieties, four were reputed to produce more stable yields across a range of environmental conditions. Over the course of three days, starting on a Thursday in December, Bradshaw planted 1,700 seeds of each variety in plots of equal area at three spacings: 12", 6", and 4" apart. Four months later, on a Saturday in April, the barley started to come to head. Over the next few weeks Bradshaw measured ten quantitative characters on each plant (Table 2). Bradshaw's statistical model focused on varietal differences in both the mean and variance among *treatments*, among *individual* plants, and *within* individual plants.

There are three notable contrasts between Bradshaw's experiment at Davis and his earlier experiments at Bangor. First, he switched from the rampantly outbreeding bentgrasses to barley, which was largely self-fertilizing. Second, instead of testing responses to fertility and moisture, he focused on responses to planting density. Third, rather than simply comparing means among treatments and populations as he had done in the 1950s, Bradshaw compared both means and variance, and at three different levels: the response of

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varieties to contrasting densities, variation in response among individuals within those varieties, and (for some traits) variation in response within individual plants (Table 2). Each

Table 2. Phenotypic characters measured in Bradshaw's experiment at Davis, 1963–1964.			
	Within Plant	Between Plant	Between Treatments
Components of Yield			
Initial tillers		✔	✔
Fertile tillers		✔	✔
Seed number/tiller	✔	✔	✔
Seed size	✔	✔	✔
Total seed number		✔	✔
Total seed weight		✔	✔
Other correlated characters			
Internode length	✔	✔	✔
Leaf length	✔	✔	✔
Height of tillers	✔	✔	✔
Ear emergence	✔	✔	✔
Transcribed from Bradshaw's notebooks (D1041/2/15).			

of those shifts are significant for understanding Bradshaw's ideas about plasticity.

3.4.1. The Material: Barley

The impetus to use a self-fertilizing cereal like barley, rather than the outbreeding bentgrasses on which Bradshaw had focused for over a decade, likely came from Allard.

Robert Wayne Allard (1919–2003) was born into a farming family in the San Fernando Valley, California. As a child, he was inspired by UC Berkeley plant breeder W. W. Mackie. He studied agriculture at the University of California at Davis, starting in 1937, where he was influenced by the prolific cereal breeder Coit Alfred Suneson (1903–1976). As a Ph.D. student at the University of Wisconsin, Madison, Allard was influenced by theoretical population geneticist Sewall Wright. In 1946, Allard returned to Davis as an assistant professor of agronomy, and as an assistant geneticist in the Agricultural Experiment Station where he was responsible for bean breeding (Clegg 2006).

Allard's research on lima beans and barley in the 1950s and 1960s challenged Stebbins' model of evolution in self-fertilizing plants. Stebbins' model of evolution in inbreeders predicted that natural populations of self-fertilizing plants should be composed of reproductively isolated homozygotic lines. Occasional interbreeding between those lines would, according to Stebbins' model, produce new heterozygotic variants that would undergo selection and form new inbred lines (Stebbins 1950). But Allard demonstrated, both theoretically and empirically, that even low levels of outbreeding (2 to 5%) were enough to maintain both a high level of genetic variation and a high level of heterozygosity (Jain & Allard 1960, Allard & Jain 1962, Allard & Workman 1963, Workman & Allard 1964). Allard's work opened up the range of possible approaches to breeding crops like oats, beans, and barley.

Allard advocated a "bulk population" approach to plant breeding that, he contended, was better suited to changing environmental conditions and agricultural practices, such as the increasingly intense use of fertilizers. Because breeders focused on isolating a small number of "high value" genotypes, Allard argued, the resulting strains were left with too little genetic variation to respond to further selection (natural or otherwise) (Allard 1961). Allard thought that instead of focusing on refining intensively-selected strains of barley and their potential hybrids, breeders should maintain highly diverse "composite cross" populations, crossing-in material from many different genetic backgrounds. Consequently,

Allard was very interested in sourcing and conserving genetic variation from the wild progenitors of cultivated crops.[81]

Under Stebbins' model, in which self-fertilizers were thought to partition themselves into reproductively isolated homogenous lines, the "bulk population" approach would have been a waste of time. But if even low levels of outcrossing could maintain significant admixture, as Allard had shown, his approach would have multiple advantages. First, it would allow a much greater number of new combinations of genes to come together over time, and form complex interaction systems that would produce new, potentially valuable phenotypes. Second, it would permit a continued response to selection in the long run, due either to changing environments or to new breeding objectives. Third, it would lead to more stable yields in the face of environmental fluctuations.

3.4.2. The Independent Variable: Density

Whereas Bradshaw's early experiments focused on responses to soil moisture and fertility, his barley experiment focused on responses to planting density.

One source of Bradshaw's interest in density was Harper's work on the effects of planting density on yield. Harper's broader research program during this period focused on the effects of plant interactions on the composition of plant communities (Harper & Chancellor 1959, McNaughton & Harper 1960, Harper *et al* 1961, Sagar & Harper 1961). Harper found that, in both wheat and beets, yield was often highest at intermediate densities, driven by changes in seed output and growth habit at the level of individual plants

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[81] Like many of Bradshaw's colleagues, Allard was a member of a small community of agro-ecologists who participated in the United Nations Food and Agriculture Organization's technical conferences on plant genetic resource conservation in the 1960s.

(Harper 1960, Harper & Gajic 1961). In other words, population density and reproductive output were regulated in part by phenotypic plasticity.

The relationship between planting density and yield had clear consequences not only in the field, but also for genecological research at the WPBS. WPBS genecologists had long conducted common-garden experiments and varietal field-trials using a spaced-plot design, in which individual plants were grown at very low density. But Alec Lazenby, in the Grass Breeding Department, was finding that high-performing strains of forage grasses in the spaced-plot trials often fared quite poorly under higher-density broadcast seeding in pastureland. In experiments with genetically identical clones of *Lolium perenne*, Lazenby found that the response to density could vary widely among individual genotypes (Lazenby & Rogers 1962, 1964, 1965a, 1965b).

Bradshaw saw density as a "cheap" environmental variable (in the sense that it could be manipulated easily), but one with considerable agroeconomic significance. Bradshaw wrote that, "Since crop-density is not always precisely controlled, response to unavoidable fluctuations in density is of economic importance" (Bradshaw 1964, p.122). From about 1960 to 1963, Bradshaw's student Mazoor Ahmed Khan studied varietal differences in linseed and flax, including their responses to density (Khan 1963). That project set the stage for later experimental studies by Bradshaw and his students.

3.4.4. The Dependent Variables: Stability and Plasticity

Bradshaw's original conceptualization of phenotypic plasticity was squarely genecological: if local populations are adapted to the particular habitats in which they are found, and if the ability to respond to fluctuations in environment via alterations of phenotype is a component of that adaptation, then the salient empirical problem was to

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demonstrate that populations differ hereditarily in the nature or magnitude of their phenotypic response to environmental differences. Yet Bradshaw's experiment at Davis went beyond comparing changes in varietal means to contrasting environments. His experiment was designed to characterize differences not only in means, but also in variances, *among treatments*, among *individual* plants, and *within* individual plants. This shift represented an attempt to bridge two distinct investigative contexts: one surrounding the developmental-genetic causes of phenotypic stability, in which the concept of phenotypic plasticity was entrenched at the time, and the genecological approach in which Bradshaw was trained.

One of Allard's arguments for the composite-cross approach to plant breeding was that the resulting strains would produce more stable yields. Allard thought that the mechanisms underlying stability were twofold. First, at the population level, different genotypes would respond to environmental changes in different ways, so that negative and positive changes in yield would balance each other out on average. Whereas genotype-environment interaction would be a source of instability in a homogeneous variety, in a genetically diverse population it would promote overall stability. Second, high genetic diversity would mean higher levels of heterozygosity. Allard thought that high heterozygosity provided more numerous opportunities for "balanced gene complexes" to emerge, producing individual plants with much greater phenotypic stability (Allard 1961).

Allard's thinking about stability tracked a broader debate among population geneticists at that time. An open question among population geneticists in the 1940s was how populations could persist in the face of environmental change. Allard shared the view of Theodosius Dobzhansky (1900–1975) and others that high levels of standing genetic variation in natural populations facilitated adaptive evolutionary responses to environmental fluctuations (Dobzhansky & Levene 1955). But this raised the question of how such high

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levels of genetic variation—or "balanced polymorphism"—were maintained in the first place since, all else being equal, natural selection alone could only reduce variation.

Dobzhansky's collaborator Isadore Michael Lerner (1910–1977) proposed an account of "genetic homeostasis" in 1954 that connected population-level responses to environmental change to developmental-genetic mechanisms in individual organisms (Lerner, 1954; Hall, 2005). According to Lerner, genetic variation was maintained by the tendency for heterozygous individuals to have greater fitness than their homozygous counterparts, a phenomenon called "heterosis."[82] To explain heterosis, Lerner suggested that heterozygous individuals are more developmentally stable (Lerner 1954). That is, they are able to develop normally under a broader range of environmental conditions than their homozygous counterparts. On short time-scales, environmental fluctuations favor more stable, heterozygous individuals, which maintains the genetic variation needed for population-level adaptation to fluctuations on longer time-scales. The centrality of heterosis to Lerners' and other accounts led to a great deal of research and debate about the mechanisms linking heterozygosity to developmental stability, which Thoday called "phenotypic flexibility."

For Thoday, Bradshaw, and others involved in this field the concept of developmental stability was linked to the notion of developmental buffering, or

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[82] So-called "hybrid vigor" had indeed been documented even in the 19th century, and was elaborated by geneticists George H. Shull and Edward M. East in the 1900s and 1910s (Paul, 1994). In the 1930s, mathematician R. A. Fisher had identified heterozygote advantage, "heterosis" (as Shull and East called it), or "overdominance" as a source of equilibrium in population genetic models: the inflated fitness of heterozygotes prevented any one allele at a given locus from going to fixation. The extent to which heterozygote advantage occurred in nature became a central point of contention in the infamous "classical/balance controversy" between Dobzhansky and H. J. Muller (1890–1967) during the 1950s and 1960s (Beatty, 1987).

"canalisation," proposed by embryologist Conrad Hal Waddington (1905–1926). According to Waddington, the phenotypic stability of wild varieties was the result of "epigenetic" systems that tracked development along well-constrained pathways, counteracting the destabilizing effects of environmental fluctuations (Waddington 1957). Waddington thought that canalisation helped to explain "how the genotypes of evolving organisms can respond to the environment in a more co-ordinated fashion" (Waddington 1942).

Disagreement among geneticists about the relationship between heterozygosity and stability revolved around two main issues.

The first issue was what it meant for organismal development to be stable or unstable, and thus what developmental-genetic mechanisms might explain it in principle. Some researchers, including Forbes W. Robertson and E. C. R. Reeve at the Institute of Animal Genetics in Edinburgh, thought that the stability of heterozygotes was a result of having a greater number of available developmental pathways (Robertson & Reeve 1952). Similarly, Lerner speculated that heterozygotes were more stable than homozygotes because, at many loci, they possessed two alleles rather than one, permitting a wider range of biochemical interactions under different environmental conditions (Lerner 1954).

On the other hand, Kenneth Mather (1911–1990) at the Agricultural Research Council's Unit of Biometrical Genetics at Birmingham, thought that the instability of homozygotes was caused by a disruption of complex gene combinations (present in heterozygotes) that had been tested and honed by natural selection (Mather 1950). Dobzhansky shared that view (Dobzhansky & Wallace 1953). Mather and geneticist John L. Jinks (1929–1987) reported that hybrids among inbred lines of *Nicotiana rustica* showed no less variability than their more homozygous parents, although levels of variability were highly heritable (Jinks & Mather 1955). Contra Lerner, this suggested that it was not heterozygosity

per se that was responsible for stability, but rather the coming together of particular combinations of alleles. Given a paucity of direct evidence about the mechanisms connecting specific genes to specific patterns of phenotypic variation, however, there was a great deal of latitude for theorizing and semantic squabbles (Lewontin 1957).

The second problem was how to measure organismal stability. Thoday thought that intra-organismal symmetry—such as in the number of bristles on the abdomen of individual *Drosophila*, or in their wing morphology—was a corollary of developmental stability, and could therefore be used as a metric (Tebb & Thoday 1954, Thoday 1955, 1958). In contrast to Thoday, Dobzhansky's student Richard Lewontin argued that if stability were conceptualized as an adaptation, the only defensible operational measure of stability was fitness itself: the genotype with the highest average fitness across a range of environments should be considered the most stable (Lewontin 1957).

Allard's ideas about the link between heterozygosity and stability stemmed in part from his collaboration with Jinks and Mather. Allard worked with Jinks and Mather on the quantitative genetics of *Nicotiana* while on sabbatical at the University of Birmingham in 1954 and 1955 (Allard 1956).

Although Thoday, Lewontin, and others looked for individual traits or quantities that could serve as measures of stability, following Waddington they tended to see stability as a feature of the organism as a whole. Lewontin (1957), for example, referred to the importance of a "harmonious balance" within the organism. In his correspondence with Bradshaw, Thoday emphasized that organisms might adjust many different physiological and morphological traits to achieve survival to reproduction under adverse conditions. Those researchers looked inward, to the structural relations and complex interactions of

developmental-genetic and physiological mechanisms to explain the link between heterozygosity and stability.

The fact that Bradshaw saw Thoday's conception of plasticity as a starting-point for his own work forced him to reconcile a discourse about internal mechanisms underlying whole-organism stability with a genecological epistemic framework focused on adaptive relationships between specific traits and specific environmental factors. In March, 1961, he confided to Ken Lewis at the Oxford Botany School that, "There seem to be so many facets of [the subject of plasticity] that it is difficult to know exactly what terms to use and almost where to begin" (D1041/4/3/21).

Bradshaw and Allard's shared interest in stability explains Bradshaw's choice of barley varieties. He sought a contrast between those well-adapted to the prevailing climate and those that were not, and between stable and unstable varieties (Table 1). The comparison between the "Vaughn" and "Atlas" varieties was particularly compelling. One of Allard's regular correspondents, crop geneticist Keith Warren Finlay in Australia, reported that those two varieties differed radically in their degree of stability: whereas Atlas gave more consistent yields from year to year, Vaughn was highly erratic. On the other hand, Vaughn was by far the superior producer under optimal conditions. Bradshaw thought that breeding for high yield might have caused a breakdown in stability, which would explain Finlay's observation.

Bradshaw's experimental design was one attempt to draw the concept of phenotypic plasticity from within the debate about stability into a genecological epistemic framework. Differences in varietal means between treatments would indicate differences in plastic response, while variance among individuals would indicate degree of stability. By analyzing variation among and within individual plants, Bradshaw could tease apart population-level

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stability from individual-level developmental stability. By scrutinizing correlations among responses to planting density in various traits, he could demonstrate not only that stability and plasticity varied among populations, but that plasticity or stability in a trait could vary *independently* of other traits.

Bradshaw was not alone in his attempt to reframe the concepts of plasticity and stability as genecological concepts. In the spring of 1964, Bradshaw gave a seminar about metal tolerance at the University of Oregon, where he was hosted by botanist Stanton A. Cook (b. 1929) and his wife, Joan. Cook, son of physiologist and anthropologist Sherburne F. Cook (1896-1974), studied under Lincoln Constance and Herbert Baker at the University of California, Berkeley. Cook's dissertation research focused on variation and local adaptation in *Eschscholzia californica* in California and Oregon in the late 1950s (Cook 1960). Like Bradshaw, Cook found that adaptive differentiation could occur on very small spatial scales (Cook 1960). After moving to the University of Oregon in 1960, Cook turned his attention to the relationship between local adaptation and developmental flexibility in the water buttercup *Ranunculus flammula* (Cook 2013a).[83] Cook wrote a grant proposal to the National Science Foundation, awarded in 1962, in which he proposed to study adaptive differentiation in heterophylly (environmentally-induced variation in leaf morphology) in *Ranunculus* at various spatial scales in western Oregon (D1041/4/3/8). In addition to addressing the relationship between population-level and developmental flexibility, Cook asked whether adaptive plastic responses were linked to heterozygosity (D1041/4/3/8).

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[83] Cook visited Turesson at Uppsala en route to the 11th International Congress of Genetics at the Hague in 1963, and saw some of the same populations of Ranunculus that Bradshaw had seen in 1950.

Oddly, Cook and Bradshaw did not discuss their ideas about plasticity during Bradshaw's visit in 1964 (Cook 2013b) and so, when Bradshaw sent Cook a draft of his review on the topic later that year, Cook expressed his surprise that their "thoughts ha[d] been running along the same tracks in parallel" (D1041/4/3/9). Between 1963 and 1967 Cook and his graduate student, Michael P. Johnson, found that populations of R. *flammula* could evolve divergent plastic responses to environmental variation over distances as short as four meters, and that plasticity in different traits could evolve independently (Cook & Johnson, 1968). Bradshaw drew on Cook's grant proposal, and the extensive comments that Cook made about his draft manuscript, in developing the final version of his 1965 review (D1041/4/3/9).[84]

The results of Bradshaw's experiment at Davis were never published. Bradshaw's notes and correspondence, however, indicate that the results were strongly suggestive that the plasticity and stability of some traits could vary independently. In a grant proposal to the Agricultural Research Council in 1964 (described below), he wrote that,

> I believe that plasticity is under genetic control and that it is a property of individual characters. It seems likely that we will find that, as an outcome of natural selection, some characters, such as leaf area and tiller number, are allowed to vary, while other characters such as seed and flower size are held extremely constant. (D1041/4/3/2, p. 3).

That statement became a crucial premise of Bradshaw's 1965 review, which, after many years of planning, he drafted on the trans-Atlantic voyage back to Bangor in mid-1964.

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[84] Cook's contributions to Bradshaw's 1965 review includes Bradshaw's opening passage, a 1914 quote from Hans Nilsson-Ehle. Cook had translated the quote and included it in his own 1961 NSF grant proposal.

3.5. An Empirical Research Program

Bradshaw's work on phenotypic plasticity was as much an empirical project as it was theoretical. His experimental work on plasticity started in the late 1950s, many years prior to his famous 1965 review. It was not until his experiment at Davis in the early 1960s that Bradshaw felt confident to bring his long-anticipated review paper to light, and to make a serious attempt to secure funding for further empirical research on plasticity. At that time, Bradshaw thought that his work on mineral nutrition in grasses was coming to a close, and that experimental studies of plasticity represented the next major direction for his research (D1041/4/3/2, p.4).

While still at Davis in 1964, Bradshaw drafted a proposal to the Agricultural Research Council for an investigation of phenotypic plasticity in crop plants and their wild progenitors. Bradshaw's proposal revolved around four questions:

Given a variable environment:

I) Can different populations of a species differ in their ability to cope with such variation in environment?

II) How is this ability manifested in different characters? Are certain characters held constant and others allowed to vary, or is the whole organisation of the individual involved?

III) What is the contribution of different characters? Is the same end point of adaptation achieved in different ways by different genotypes?

IV) If populations of a species do differ in their ability to adjust to variation in environment, what is the genetic basis of such differences?

(D1041/4/3/2, p.2)

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The project outlined in that proposal was to build on work by Bradshaw's student Mazoor

Ahmed Khan concerning responses to density in linseed and flax, this time focusing on both

wild and cultivated varieties of sunflower (*Helianthus annuus*), soft brome grass (*Bromus mollis*),

domesticated barley (*Hordeum sativum*), and wild barley (*Hordeum spontaneum*). The grant would

also fund M. Akram Khan's ongoing doctoral research on response to density in *Linum*

(Khan 1967). Bradshaw justified the project with reference to its agricultural consequences.

In his proposal to the A.R.C., Bradshaw wrote that, "In agricultural crop varieties, where the

genetic composition is held constant artificially, adaptation to the varying conditions of one

year and another can only be met by plasticity," but that "we do not know a great deal about

the subject despite its immediate relevant to agricultural practice." (D1041/4/3/2, p.1)

Although there is no evidence to suggest that the A.R.C. funded Bradshaw's project,

much of the proposed work was ultimately carried out. At least three of Bradshaw's graduate

students, Muhammed Akram Khan, Muhammed Iqbal Khan, and Peter Kyle, conducted

experimental studies of plasticity and canalisation in flax, linseed, sunflowers, and tobacco

(Khan 1967a, Khan 1967b, Kyle 1966, D1041/4/15). That they were carried out even in the

absence of external funding suggests that Bradshaw was committed to serious and sustained

experimental studies of plasticity.

Bradshaw's work on plasticity attenuated sharply after 1968. There are a variety of

plausible reasons for this, including a change in the funding landscape that brought

Bradshaw's work on heavy-metal tolerant plants back to the foreground. In 1966, over one

hundred forty people (mostly children) in the mining town of Aberfan in South Wales were

crushed by material from a coal-mine waste tip that was destabilized by heavy rains (Couto

1989). The Aberfan disaster created a strong political imperative to reclaim old industrial

waste and mining sites around Britain (House of Commons 1967, Goodman 1974) amplified

by passage of the Mines and Quarries (Tips) Act of 1969. Bradshaw was soon approached by representatives of the copper industry, and found it much easier to find funding for restoration-related research (Jowett, pers. comm.). Those events coincided with an offer from the University of Liverpool to assume the Holbrook Gaskell Chair of Botany, which Bradshaw accepted in 1968. Bradshaw's willingness to move away from his work on plasticity may also have stemmed from difficulties in analyzing his data and publishing the results of his students' research.[85] All of those factors likely conspired to shift Bradshaw's attention to what would later be called "restoration ecology" (see Sarkar 2011).

3.6. Discussion

Bradshaw work on plasticity was not unprecedented. Moreover, his account of plasticity was not at all a shift from a gene-centric epistemology to one concerned with the interaction of heredity, developmental processes, and environmental context. In fact, such an interaction-oriented perspective was already alive and well when Bradshaw joined the fray. Bradshaw's model should be understood instead as a response to an ongoing discourse about plasticity, stability, and yield. Indeed, it can be seen as a reformulation of a structural, inward-facing, whole-organism conception of phenotypic plasticity into a functional, outward-facing one.

The collaboration between Bradshaw and Allard at Davis in the early 1960s, which catalyzed Bradshaw's influential 1965 review, represented the confluence of two extant lines of investigation: the agro-ecological tradition of British genecology, on one hand, and a lively

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[85] Some reviewers did not respond well to submissions based on his students' projects. The problems noted by reviewers, as well as delays in analyzing the data from his experiment at Davis, appear to have stemmed from difficulties in performing and interpreting appropriate statistical analyses. Some of the work from this period was ultimately published in the late 1970s after substantial revision, as Khan & Bradshaw 1976 and Khan *et al.* 1976. Other manuscripts, such as one concerning canalisation of seed size in *Helianthus* based on M. Iqbal Khan's research, were never published (D1041/4/15).

exchange among population biologists about the evolutionary and developmental-genetic relationships between heterozygosity, phenotypic stability, and developmental canalization on the other. Bradshaw re-cast questions about developmental stability within the epistemic framework of British genecology: he appealed to specific external selective pressures on specific traits, rather than the internal structural organization of whole organisms, to explain differences in stability and plasticity among populations of organisms.

The importance of a genecological epistemic framework for Bradshaw's ideas about plasticity is reflected in his assessment of Finlay and Wilkinson's (1963) method for evaluating the relative stability of crop varieties, described by Baranski (2015):

> In this respect the regression technique for the analysis of phenotypic
>
> response, introduced by Finlay and Wilkinson (1963), where the environment
>
> is measured by the mean growth of all the different genotypes being assessed,
>
> has almost been too successful, because it has allowed us to escape from
>
> measuring the specific attributes of the environment which are causing
>
> phenotypic change. (D1041/4/15/1/5)

Bradshaw's approach to adaptive phenotypic plasticity was an attempt to operationalize it as an investigable phenomenon within a research framework that was focused on adaptation by natural selection in natural populations. Bradshaw thus directed attention away from internal mechanisms and toward the external relations action of natural selection in molding and fine-tuning phenotypes. In the genecological framework this meant attending to specific environmental factors, something that the Finlay-Wilkinson method obscured.

Understanding the theoretical context for Bradshaw's ideas about plasticity sheds some light on what Bradshaw meant when he said that plasticity in specific characters could be under "direct genetic control." In his 1965 review, he wrote:

> It can be argued that the plasticity of a character is related to the general pattern of its development, and apart from this, that plasticity is a general property of the whole genotype. A review of the evidence suggests that neither of the conclusions is tenable. Plasticity of a character appears to be (a) specific for that character, (b) specific in relation to particular environmental influences, (c) specific in direction, (d) under genetic control not necessarily related to heterozygosity, and (e) able to be radically altered by selection. (Bradshaw 1965, p. 149)

The meaning and epistemic implications of "direct genetic control" became a flash-point for controversy in the 1980s and 1990s. In particular, population ecologists Sara Via and Samuel Scheiner disagreed loudly about the existence (even possibility) of so-called "plasticity genes" that operate independently of those responsible for controlling mean trait values in populations (Nicoglou, this issue). Bradshaw was not making claims about plasticity genes, *per se*, but was mainly focused on replacing the whole-organism conception of plasticity and stability with one that could be investigated in a genecological framework. In the same vein, he resisted Stebbins' (1950) claim that, in Bradshaw's (1965) words,

> ...characters formed by long periods of meristematic activity (such as over-all size, leaf number, etc.) will be more subject to environmental influences and are likely to be more plastic than characters formed rapidly (such as reproductive structures) or than characters whose pattern is impressed on

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primordia at an early stage of development (such as bud scales, leaves, etc.).

(Bradshaw 1965, p. 117).

Bradshaw did not completely reject Stebbins' views on plasticity, but did seek to emphasize situations in which plasticity was not so tightly restricted by developmental constraints.

In attending to the practices and richness of discourse surrounding adaptive plasticity in the mid-20th century, this paper contributes to an expanded historiographical framework for evolutionary biology that both enriches and transcends the Modern Synthesis narrative. Work by Provine (1971), Bowler (1983), Smocovitis (1996) and others (e.g., see papers in Mayr & Provine 1980, and Grene 1983) have thoroughly documented the efforts of some influential biologists in the 1930s and 1940s to establish a discipline of evolutionary biology that was centered on population studies and undergirded by theoretical population genetics. Subsequent work has emphasized the complex relationships between the Synthesis project and the diverse evolutionary research traditions that spanned that period (e.g., see chapters in Cain & Ruse 2009). Bradshaw's model of adaptive plasticity was shaped by his attempt to operationalize theories of developmental organization within a particular set of research practices. In Bradshaw's case, we can see the significance of the genecological research tradition for what became a highly influential contribution to evolutionary theory in the decades following the Synthesis period. Further work is needed not only to understand subsequent models of adaptive plasticity, but also to fully assess the impact of the genecological research tradition on the development of 20th-century evolutionary theory.

CHAPTER 4. HATCHING THE EGG

4.1. Introduction

The history of scientific fields is built on books and societies. Demarcating a scientific field, and identifying the times and places of its emergence and expiration, is a task analogous to the delimitation of biological species and other units of evolution. The questions, hypotheses, and imaginations pursued by scientists are extremely diverse, varying according to the peculiarities of each investigator's training, experiences, and personal style. The historian's challenge is to find the currents in that sea of variation, grouping investigations together in a sensible ways, such that some greater explanatory power is achieved.

Part of this task is to understand how scientists themselves cut up the project of understanding the natural world. As Kingsland (2008) suggests, scientific disciplines and fields are not woven into the fabric of reality, but are generated and molded by the aspirations of scientists and the social and material contexts in which scientists operate. The construction, by scientists, of a field or discipline is a way of enforcing epistemic norms; of deciding what counts as proper and valuable scientific questions, and what evidences can and should be brought to bear on those questions. For many historians, discipline-formation in the Kuhnian sense is more of a narrative act than a logical one. Smocovitis's (1996) history of the Modern Evolutionary Synthesis, *Unifying Biology*, is written from that standpoint.

Thomas Kuhn's 1962 book, *The Structure of Scientific Revolutions*, focused attention on the discontinuity of scientific fields, and how older paradigms yield catastrophically to newer ones. The causes of such paradigm shifts are, according to Kuhn, twofold: the weight of accumulating evidence signifying the inadequacy of the older paradigm's theoretical structure, and the forceful assertion of a new set of theories and practices by a younger

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generation of scientists. The forceful assertions and narrations of discipline-builders usually manifest themselves in books, and thus the historian justifiably looks to influential and agenda-settings texts to mark the start and the end of scientific fields. We learn much about the emergence of evolutionary biology as a discipline, for example, by looking to Theodosius Dobzhansky's (1937) *Genetics and the Origins of Species*, Julian Huxley's (1942) *Evolution: The Modern Synthesis*, and G. Ledyard Stebbins' (1950) *Variation and Evolution in Plants*. It is unsurprising, then, that we should look to E. B. Ford's (1965) *Ecological Genetics* as an inflection point for the emergence of the scientific field of the same name.

Whereas a history of books yields a discontinuous view of scientific change, the manners and contexts in which scientists associate with each other suggests a more continuous evolution. Ludwik Fleck's (1935) *Entstehung und Entwicklung einer wissenschaftlichen Tatsache* drew attention to the role of exchanges among individual scientists in shaping scientific language, norms, and fields. When scientists interact they gradually form new specialized patterns of language and thought that both inform and constrain the direction of research. Another way to demarcate fields, therefore, is to look for those scientific "collectives" and analyze their "styles" of thought and communication. Attending to the formation and evolution of scientific societies can provide a lens onto how scientists associate with each other, and what comes of those associations.

An important chapter in history of the field of ecological genetics, therefore, is the story of the Ecological Genetics Group. The EGG is perhaps the foremost gathering for ecological geneticists in Britain. The annual meeting of the EGG, around Easter, usually runs for two or three days and places special emphasis on graduate student work. Since 1988 the British Ecological Society has recognized the EGG as a Special Interest Group. On 30 March – 1 April, 2015, Dr. Paul Ashton will host what its members consider to be the 59th

meeting of the EGG at Edge Hill University in Liverpool. The EGG traces its beginnings to a gathering of plant ecologists from the Scottish and Welsh Plant Breeding Stations in 1956. As I described in chapter 2, the purpose of that meeting was to facilitate a meeting between Tony Bradshaw and Dennis Wilkins concerning their work on lead tolerance in *Agrostis*, and to allow for general exchange among the staff of the Genecology Section at the SPBS and the Grass Breeding Department at the WPBS. This meeting was repeated in subsequent years and, in 1960, attendees dubbed themselves the Ecological Genetics Group.

The history of the EGG provides a clear link between the genecological practices at the SPBS and WPBS, Bradshaw's early investigative activity, and the subsequent development of ecological genetics in Britain. In this chapter I describe the origins of the EGG in greater detail. First, I summarize the context and circumstances leading up to the first meeting of the group, described more extensively in chapter 2. I then describe the content of the 1960 meeting, and the rationale for forming a more substantial organization. I then describe some of the ways in which the EGG grew and diversified over the next several decades.

4.2. Conception

The 1956 meeting of the Fellows of the National Institute of Agricultural Botany (NIAB) was to be held in July, 1956. E. T. Jones was to receive the NIAB Cereal Award for his "Powys" variety of winter oats, and to confer with NIAB leadership about the ongoing transfer of grass and clover seed stocks from the WPBS to NIAB. For members of the SPBS, the annual NIAB meeting was seen as an obligation. "All the plant breeding stations had to get together each year," one of the Genecology Section staff, David Harberd,

recalled, "and you didn't have any choice in the matter: you went. The bosses in London just decided where you were meeting and you went" (Harberd pers. comm.).

As the NIAB meeting approached, however, circumstances were extraordinarily complicated for Harberd. Harberd's wife, Muriel, had dropped six stone (over 80 pounds) due to complications with her pregnancy, and was still recovering as the NIAB meeting approached. So several days before the trip to Cambridge, Harberd approached Gregor and asked to be excused from the meeting.

"I cannot leave Muriel just now," Harberd explained, "She's gone through such a hell of a time, and I must be here for her."

Gregor assured Harberd that he would sort things out so that he could be excused. Suspecting that there was more to the story, however, he probed Harberd further. "I don't think you *want* to go, do you?" Gregor asked.

"Of course I want to go," Harberd replied, "It's jolly good, but I just don't want to be away from home." After all, he had lived in Cambridge for several years prior to moving to Edinburgh, and many of his friends remained in the area.

Gregor pushed further: "Well now, what benefits do you think you get from these [meetings]?" Harberd replied:

Well, it's just social. There's nobody there will be working on grasses. Last time when we were all over in Belfast, we had to go through flax breeding. Well there wasn't a single person there who knew anything about flax breeding apart from these folk. And it was fascinating to learn their problems and how they were tackling them, but we couldn't contribute. Really, it just so happened that it was fascinating, but if we're going to have a session on breeding watercress or something, I can't imagine how

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we're going to -- I mean it's is a different kettle of fish altogether. I really think the money would be much better spent if, instead of the whole station decamping like that, we had an arrangement whereby all the potato breeders could gather together every so often and exchange gossips. And the barley breeders could do this, and all the grass breeders could do this. It would be cheaper, and it would be far more efficient, and we'd really make some progress. (Harberd pers. comm.)

So upon arriving at Cambridge, Gregor mentioned Harberd's idea to Keith Jones, who had accompanied E. T. Jones from the WPBS. Jones was quite interested in a meeting specifically focused on grasses and grass breeding. Gregor was also fascinated to hear of Bradshaw's ongoing work on lead tolerance in *Agrostis*, for one of his own staff members, Dennis Wilkins, had undertaken similar studies on mine tips in Lanarkshire after reading of Bradshaw's 1952 discovery at Goginan mine. Jones and Gregor agreed to convene a meeting that would bring the staffs of their two departments together and provide an opportunity for Bradshaw and Wilkins to compare notes.

Gregor wrote to Jones around a month later to concretize their plans. "When we met at Cambridge I told you of the wish of our genecological group to pay Aberystwyth a visit some time this autumn," Gregor wrote, "to see the work you and your colleages are doing with the wild grasses, and you very kindly agreed to have us. […] You will remember that the suggestion was to get Bradshaw down to Aberystwyth at the same time so that we might hear about his latest work on *Agrostis*, and particularly to give Wilkins an opportunity to discuss with him the lead tip flora and, if possible, to visit some of the tips in his company" (D1041/2/9/22/2). Gregor proposed a meeting on a Wednesday, the 26th of September, with a field trip to the mine tips on Thursday. Jones passed the letter on to

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Bradshaw, writing, "I had some prolonged discussions with him at Cambridge some time ago and he is very keen to visit us. He would particularly like you to be here if you can manage it both to hear of your gene-ecological stuff and for you to take Wilkins to the lead mine areas. Watson has some interesting information on hybridisation of Agrostis under natural conditions, and I have no doubt that we should profit by discussions with them" (D1041/2/9/22). Upon hearing back from Bradshaw, Jones replied to Gregor enthusiastically. "I had not forgotten about your desire to visit the W.P.B.S.," Jones wrote, "and indeed we shall be looking forward to seeing you and your part. For the past month I have been trying to get in touch with the elusive Bradshaw, and at last today I received a letter from him from Fort William, where is is on holiday. As far as I can make out he will be able to come here on the 26th September. This date is also suitable for [Martin] Borrill and myself, although Mr. [Arthur R.] Beddows will probably not be here." (NLW ex 2747).

So Gregor, Harberd, Wilkins, and Patricia Watson traveled to Aberystwyth. Gregor and Wilkins passed the time by playing chess in their booth. Bradshaw came down from Bangor on his green motorbike with David Jowett, who had recently arrived from Liverpool, riding on the back. The Edinburgh party arrived at the Aberystwyth train platform in torrential rain. In 1955 the WPBS had moved its operations from its hillside campus at Penglais to a site further east at Plas Gogerddan, so none of the visitors knew which bus to catch. After asking around for directions, navigating buses, and walking in the rain, they eventually arrived at the white mansion at Plas Gogderddan that housed the new administrative offices of the WPBS. They spent the day exchanging notes, catching each other up on their latest research. That night, Harberd and Bradshaw stayed with Keith Jones at his on-campus house, named "Oregon"; when they arrived for dinner that evening,

Bradshaw quipped jokingly, referring to the Oregon-R strain of *Drosophila melanogaster*, "Oh, Oregon. That's a place for a wild type to live" (Harberd pers. comm.).

The visit was deemed a success, and promises were made to reconvene the following year. In April of 1957, Pat Watson wrote to Keith Jones inviting the WPBS contingent to visit Edinburgh late that summer. "We hope that you and some of your colleagues will be able to come visit us this year," Watson wrote, "and that the meeting will prove to be as interesting as we found our visit to Aberystwyth last September. As always happens, the summer months promise to be very busy but since we understand that some of you might

Figure 4.2.1. Plas Gogerddan, site of the WPBS from 1950. Courtesy of the National Library of Wales.

be interested in the Edinburgh Festival also, I am writing to propose a two-day visit sometime between 15th and 20th August" (NLW ex 2747).

A third meeting was held at Bangor the following year, this time in late March or early April. Bradshaw sent the invitation for a fourth meeting to Gregor on 17 January, 1959. "We would be very pleased indeed if we could hold another of our informal discussions this Easter. We would all be very delighted to see you down here. ... Keith Jones is in Canada so we would not have him with us, but we would hope to have at least Borrill from the P.B.S" (GD449/16/6). Gregor also described the meeting as "informal" in his reply. Bradshaw's work on lead tolerance in *Agrostis* also remained a dominant part of the discussion. "Many thanks for your letter inviting our herbage group to informal discussions at Bangor," Gregor wrote, "an invitation we gladly accept. As to the date of the meeting, Wednesday, March 25th would suit us very well and I take it that day would also suit you. Wilkins, however, feels he would like an extra day to see your people about his lead resistance work. He therefore proposed travelling on Monday 23rd and spending the following day discussing the lead programme" (GD449/16/4).

The fifth meeting, in 1960, had a substantially different flavor from those that preceded it. Participation in the group increase substantially, and it was at this meeting that the group adopted the name Ecological Genetics Group and began to establish a somewhat more formal structure. In the next section, I briefly describe the content and focus of that meeting.

4.3. Incorporation

Thomas Owen Pirtchard (b. 13 May, 1932) was a graduate of the Agricultural Zoology Program at Bangor, and shortly after finishing his undergraduate degree went to work as Deputy Director of the Nature Conservancy in Wales. The Nature Conservancy was

established in 1949 with an explicit mandate of translating ecological research into public

policy for the protection of natural resources (Goodson 1993). Pritchard is credited with the

origination of the phrase "environmental education" at the 1948 conference of the

International Union for the Conservation of Nature and Natural Resources (IUCN)

(Disinger 1984). Pritchard advocated environmental education as both vocational training

for resource managers and as way to create "public awareness about environmental affairs,

with the ultimate aim of realising the conservation of natural resources and stimulating

enjoyment of the environment" (IUCN 1972, p. 1). Pritchard had worked with Bradshaw in

the mid-1950s on the genecology of *Trifolium repens* in Snowdonia, and went on to receive a

Ph.D. in 1958 from the University of Leeds for his work on the genecology of *Euphorbia*

cyparissias (cypress spurge) and *Hypericum perforatum* (St. John's wort). It is through this

association that Pritchard became acquainted with what was becoming a regular Easter

meeting of genecologists from Edinburgh, Aberystwyth, and Bangor, and during discussions

with Bradshaw became excited about the prospect of hosting such a meeting at the Nature

Conservancy office at Attingham Park, just east of Shrewsbury.

In his invitation to Gregor in March, 1960, Pritchard was candid about his desire to

address conservation issues at the meeting. Specifically, Pritchard was interested in the

conserving "the country's gene pools." He wrote,

> A few days ago, I discussed with Dr. Bradshaw of Bangor arrangements for
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> holding a meeting of people interested in evolution in natural populations.
>
> […] The meeting will be informal as usual and attended by about 20 people
>
> actively engaged in research on plant populations. It is expected that one or
>
> two short papers will be given to introduce topics for discussion and we
>
> would also like the group to give some time to discuss the conservation of

the country's gene pools, particularly old pastures and other areas from

which breeding material has been obtained in the past. (GD449/24)

Gregor expressed some trepidation about the anticipated size of the meeting. "I hope that the meeting will be able to retain its thoroughly informal character," Gregor wrote, "for it seems to us that with twenty people it shows signs of becoming just one more conference" (GD449/24).

In the end fifteen people, including Pritchard, arrived for the meeting on Monday, the 25th of April. Harberd was involved in an automobile accident prior to the meeting and was unable to attend. Gregor also missed the meeting, but the SPBS was represented by genecologist Frederick England. From Bangor, Bradshaw brought his students John Aston and Roy Snaydon. The largest contingent came from the WPBS, including Les Breese, Malcolm Calder, John Cooper, Keith Jones, and Martin Borrill. Some new faces included

Figure 4.3.1. Thomas Owen Pritchard. From the Casgliad Geoff Charles Collection. (WlAbNL)003366279. Courtesy of the National Library of Wales.

Michael Harvey, a first-year Ph.D. student at Durham, Audrey Plack from Keele, Miss K.

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Luck from Cambridge, and Nature Conservancy staffer Miss E. Copeland Watts. Jones, Borrill, and Pritchard presented papers on Monday afternoon, and Goodway, Snaydon, Bradshaw and Cooper presented their recent work the following day. (GD449/25)

On Tuesday afternoon, Pritchard turned the conservation away from research updates and toward "the conservation of ecological races and subspecies." One of the central themes of that conversation was the idea that the locally adapted plant populations, heretofore exploited by plant breeders, were a valuable natural resource and thus an important object of conservation. Pritchard drew together his notes from that conversation to write a short paper titled *The conservation of ecological races*, which was circulated internally at the Nature Conservancy. Pritchard wrote, "The great variety of distinct natural and man-made habitats occurring in the British Isles has been conducive to widespread differentiation of ecologic races in plant species. In this country, races differentiated in response to long-established agricultural and forestry management systems are, to the student of evolution, at least of equal significance as those races adapted to natural habitats which are relatively extreme in terms of edaphic and climatic conditions such as in the higher mountains and along the coastline" (GD449/25). Bradshaw's work on *Agrostis* at Port Meadow in Oxford was cited in the discussion. "As an example, Port Meadow in Oxford … has been recorded as common land belonging to the Burghers of Oxford since Domesday times and, fortunately, it still exists as a habitat where grazing pressure as a selection force has been operative for centuries. The races of grasses and other species occurring there are of special interest to the research worker and plant breeder. Extreme *Agrostis stolonifera* x *A. tenuis hybrids*, for example, exist there and further study will inevitably reveal the presence of other interesting types" (GD449/25).
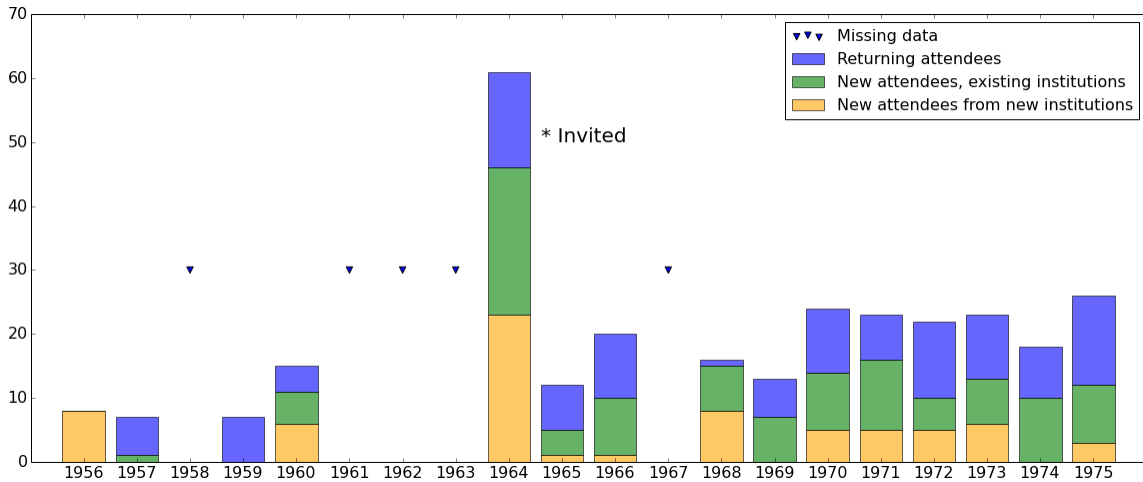
Figure 4.3.2. New and returning attendees at EGG meetings, from previously represented and new institutions. 1956–1974. Data for 1958, 1961–1963, and 1967 are not available. Values for 1964 are from a list of invitees, and are thus inflated. 1960 was a known turning-point for the group, as it was the first meeting outside of the institutions of its original participants (WPBS, SPBS, and Bangor). The group experienced further expansion in 1961, and this probably explains the high proportion of new attendees and new institutions in 1964. In 1968 the EGG co-convened with the Genetical Society of Britain, which explains the high recruitment in that year.

In his write-up, Pritchard warned about the dangers of losing habitats like Port Meadow, and the plant populations therein. "A habitat such as Port Meadow is extremely vulnerable in our time. Discounting complete destruction by ploughing or building development, it can be easily lost through simple changes in management methods. The older grazing systems are rapidly vanishing, the result being degeneration of old pasture communities and disappearance of the ecological races in them. Port Meadow still exists but there are rumours that it was recently sprayed with a chemical weedkiller to control ragwort; obviously, such a practice is bound to have devastating effects on its plant populations" (GD449/25). The group seemed to agree that "certain ecotypes and subspecies" ought to be conserved both for their value to investigations of "experimental taxonomy and evolution" as well as to provide "useful sources of genes" for agriculturally valuable characters. "It

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seems that the most urgent task at this stage is to document information on the best localities," Pritchard wrote, "and to take appropriate action after this has been considered. Members of the Ecological Genetics Group would be willing to co-operate in such a scheme." (GD449/25).

Finally, the group took up the issue of establishing a more formal structure. They agreed to meet annually, to limit the size of the meeting to "about 15 to 25 persons engaged in experimental studies on populations," and that the organizers should keep minutes from each meeting. Several names were considered: "Genecology Group" was rejected, and "Evolution Group" was also deemed unfavorable "unless the word Experimental was included." Ultimately, they adopted the name "Ecological Genetics Group." Harberd suspected later that Keith Jones might have advocated for the name, partly due to the humor of "hatching" the "EGG" around Easter time (Harberd pers. comm.).

4.4. Diversification

Whereas the 1960 meeting established the identity and purpose of the EGG, the 1961 meeting moved the EGG into a broader institutional arena. Keith Jones, who had recently left the WPBS to work at the Jodrell Laboratory at the Royal Botanical Gardens at Kew, hosted the meeting. Bringing the EGG into southern England drew in a much broader array of participants. Harberd, who had recovered from his automobile accident, remembered the gathering as "one of our most flourishing meetings. That was when we first became not a tight little group, but much wider" (Harberd pers. comm.). In addition to new faces from the research team at Kew, many others attended from the larger Universities in southern England. The well-known American botanist George Ledyard Stebbins, from California, was

visiting the UK at the time and made an appearance, along with E. J. H. Corner from Cambridge.

The earliest connections to the animal genetics community at Oxford came in 1961, albeit by way of a botanist. David A. Jones was in the second year of his Ph.D. in the Department of Zoology at Oxford. His invitation to the EGG meeting came "totally out of the blue" (Jones pers. comm.). Although Jones' earliest graduate research was in animal genetics, even involving Lepidoptera, by 1961 his interests had shifted to cyanogenesis and lectins in plants. Cyanogeneic *Trifolium* was part of Bradshaw's teaching portfolio in genetics in the 1950s, and it is possible that this shared interest, along with Jones' general interest in polymorphism and ecological genetics, were what resulted in the invitation.

Jones' continued involvement in the EGG opened the door to others from the zoology and animal genetics community at Oxford in subsequent years. For example, David William Snow, an ornithologist (Ph.D. Oxford, 1953), first attended the EGG in 1965. Entomologist John R. G. Turner (Ph.D. Oxford, 1969, Lepidoptera), and zoologist Bryan Clarke (Ph.D. Oxford, 1962, *Cepaea*) attended in 1966. Shortly after attending the EGG Clarke went on to organize the animal-oriented "Population Genetics Group," now known as PGG or PopGroup, modeled on the EGG meetings. Meanwhile, after finishing his Ph.D. in 1961, David Jones was hired as Assistant Lecturer at Birmingham. Dennis Wilkins joined the staff at Birmingham shortly therafter. This drew in more non-plant biologists from Birmingham, including Michael J. Lawrence (Ph.D. Aberystwyth, 1958, *Drosophila*) in 1965, and Michael J. Kearsay (Ph.D. Birmingham, 1965, *Drosophila*) and Giora Simchen (Ph.D. Birmingham, 1966, yeast) in 1966.

The EGG grew and diversified over the next several decades, drawing in participants

from other research groups as well as providing a "home" for the students of its central

participants. Despite Gregor's concerns about the growth of their informal annual meeting,

except on rare occasions the overall attendance remained at around thirty well into the

1970s.

Interest from David Henriques Valentine (1912–1987) in 1964 brought in a new

crop of genecologists from the University of Durham, where Valentine was then Professor

of Botany. Valentine became involved in genecological research in the 1940s, and most of

his work focused on species of *Viola*, and later *Primula*. Although Valentine's genecology

retained much of the taxonomic hue that the Gregorian school had cast aside, his interest in

abrupt versus gradual speciation was a point of intellectual overlap with Bradshaw and his

colleagues. Like Gregor, Valentine was also interested in the problem of professionalization

and institutionalization for genecology.[86] Several of Valentine's students, as well as his

colleague Jack Crosby, were invited to the 1964 meeting and became regular EGG attendees.

Bradshaw's students at Bangor made up a large part of the new recruits in the 1960s,

'70s, and '80s. John Aston, Janis Antonovics, Glenys Crossley, Peter Gregory, Thomas

McNeilly, and John Pusey all attended in 1964. As students from Bangor, Aberystwyth, and

Edinburgh took posts at other British universities they not only continued to attend EGG

meetings but also brought along their students and colleagues. For example, Antonovics

worked as a post-doctoral researcher at the University of Stirling between 1966 and 1970,

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[86] For example, Valentine took it upon himself to establish, maintain, and distribute a
directory of genecologists and their research projects in the 1960s.

and brought along several of his students, including Henry Ford, Heather Dickinson, and Joseph Watson. Roy Snaydon, who went on to work at the University of Reading and further developed the work on mineral nutrition, drew in a steady stream of students as well. Bradshaw's move to Liverpool in 1968 substantially broadened the base of attendees, as his students and colleagues joined the group. Staff and students from Aberystwyth, the Welsh Plant Breeding Station, Scottish Plant Breeding Station (later Scottish Crop Research Institute), and other agricultural research centers and provincial colleges continued to make up a large proportion of the overall attendance well into the 1990s. Over time, the EGG also attracted visitors from the European continent and North America. Bernard Dommee, who studied intraspecific variation in reproduction in *Calluna vulgaris*, was responsible for bringing in French students from Montpellier, starting in the late 1970s. Pieter Kakes, a genecologist at the University of Amsterdam, attended the meetings between 1975 and 1991, and brought along several Dutch botany students during that period.

Since 1988 the EGG has been recognized as a "Special Interest Group" of the British Ecological Society. The EGG has continued to hold its Easter-time meeting, the last of which was held 30 March through 1 April 2015, at Edge Hill University in Liverpool.

<div align="center">4.5. Conclusion</div>

One of the most striking features of the Ecological Genetics Group over the past sixty years has been its continuity with the original community of agricultural genecologists in Scotland and Wales that began meeting informally in 1956. A preliminary analysis indicates that a very large proportion of attendees over the past several years can trace their scientific "ancestry"—in terms of supervisor-student relationships—to either the early cohorts of attendees in the 1950s and 1960s. Most recent participants have been in the third or fourth

"generation" of scientists since the group began meeting in 1956. The EGG thus provides a clear continuity from the Gregorian genecology of the 1930s and '40s to contemporary ecological genetics in Britain.

The brief history of the Ecological Genetics Group offered in this chapter is a starting-point for further investigations into the evolution of British ecological genetics and evolutionary population ecology. While this account has highlighted key turning points and some qualitative trends, it leaves an open field for investigating the changing contexts, concepts, and content of ecological genetics in Britain in subsequent decades. The attendance records housed at the National Library of Wales are impressively comprehensive, and present a unique and attractive opportunity to reconstruct the history of ecological genetics in even greater detail. But with such an opportunity comes many challenges, the most notable of which is the problem of scale. Although attendance at the EGG meetings only rarely exceeded 50 people, the cumulative number of attendees since 1956 exceeds one thousand individual scientists. Moreover, the volume of research literature produced by the average ecologist has increased substantially since the 1960s. An analysis that pays adequate attention to the conceptual, methodological, and contextual dimensions of the investigative activities in which those scientists were engaged requires tools and methodologies that can scale with the volume of materials on which it is deployed. To that end, I have begun to draw together techniques from computational linguistics and social network analysis that can be applied to the history of the EGG, and other similar associations. A few of those techniques are presented in Appendix A.

CONCLUSION

This dissertation tells the story of Anthony David Bradshaw's investigation of microgeographic adaptation in populations of pastureland grasses between 1948 and 1968. Bradshaw's research during that period generated powerful new evidence that evolution by natural selection can be extremely rapid and local, and showed how the parameters of that process could be measured and studied in natural populations in real time. Bradshaw's research program contributed directly to the emergence of ecological genetics in Britain during the 1960s, and the broader project of "evolutionary ecology" that arose in the decades thereafter. The story of Bradshaw's investigative trajectory gives us a lens into the kinds of research that ushered in a new way of thinking about evolution, and into the contexts that shaped and enabled those investigations.

The central thesis of this dissertation is that a unique strain of agro-ecological research at the plant breeding stations and provincial colleges of Scotland and Wales made crucial contributions to the emergence of ecological genetics and evolutionary population ecology in the 1950s and 1960s. Ecological genetics was not the brainchild of an Oxfordian patriarch in the cloisters of establishment academe, but rather an outgrowth of multiple research traditions, one of which was the particular brand of genecology exemplified by James Gregor, further developed by Bradshaw, and magnified by the community of scholars who participated in the Ecological Genetics Group. This dissertation is not the first attempt to describe the tenets and practices of genecology in the early 20th century (e.g., Hagen 1984). But whereas foregoing accounts have focused on the emergence of genecology as an integrative and interdisciplinary field—bringing together field ecology, genetics, cytology,

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and taxonomy—this dissertation tells the story of how genecology diversified. Genecology colonized a variety of investigative habitats characterized by disparate intellectual, economic, and geophysical contexts. This dissertation tells part of the story of how those local instantiations of the genecological project diverged over time in ways that reflected those environments.

The linkage between genecology and agriculture in 20th-century Britain is significant. Although genecology was not limited to agricultural research centers, it is clear that the Welsh and Scottish Plant Breeding Stations provided a home for the distinctive flavor of genecology that most directly contributed to the emergence of ecological genetics. Paladino (2002) has discussed attempts by the Agricultural Research Council to encourage basic research in ecology and genetics at the Plant Breeding Stations in the 1940s and 1950s. Indeed, several of my own informants have described an unwritten policy at the Welsh and Scottish Plant Breeding Stations that scientific staff were permitted, and even encouraged, to pursue their own research interests using the Station's facilities and resources. Genecological common-garden and reciprocal transplant experiments required extensive resources and space both outdoors and in the greenhouse, and the Welsh and Scottish Plant Breeding Stations provided both. Moreover, they provided the material resources and workflows to carry out genecological studies. Although Gregor clearly had agricultural interests in the forefront of his mind, he frequently emphasized in his administrative correspondence that the SPBS was a center for *research* in plant breeding—addressing basic research questions with an eye to plausible applications—rather than a full-fledged plant breeding and seed

production operation. The close association of the Welsh Plant Breeding Station and the Agricultural Botany department at the University of Wales also created a hybrid environment of basic and applied research problems. It seems that this integrative or hybrid modality created a unique environment for genecological research, in which ties to agriculture informed certain biological and material aspects of the investigative activity, but an interest in producing more generalizable knowledge connected those investigations to broader theoretical problems in evolution, ecology, and genetics.

It is a working hypothesis of this dissertation that the specific problems on which the WPBS and SPBS dwelt played a substantial role in the choices that investigators made about which organisms to study, and that this in turn impacted the theoretical conclusions that ultimately emerged from the investigative activities of their scientific staffs. Historian Henry Hobbhouse (1985) has emphasized the significance of plant varieties and their biological characteristics as agents in historical and economic change, and Bruno Latour (2005) and Ian Hacking (2002) have, in various ways, drawn attention to the role of non-human causes in socio-historical processes. Genecologists at the WPBS and SPBS did indeed focus on a particular selection of plants: those herbage species significant for increasing grazing potential of derelict or upland pastures. It is not a stretch of the imagination to suppose that, had Bradshaw not chosen to work with widely distributed, rampantly outbreeding, wind-pollinated grass species like *Agrostis tenuis* and *Anthoxanthum odoratum*, he would not have grappled so directly with the interplay of strong selection and gene flow, and would therefore not have so readily come to the conclusions that he

did about the spatial and temporal scales of adaptive evolution. Although such a counterfactual supposition is beyond the scope of direct historical analysis, it does draw attention to the potential interplay of economic and biological agencies in shaping the theoretical structure of science. It is an intriguing coincidence that Hobbhouse's historiography was inspired in part by the work of R. George Stapledon at the Welsh Plant Breeding Station (Hobbhouse 1985, pp. xiii–xv).

Why did Bradshaw change his mind about the speed of organic evolution? And why did so many ecologists like him adopt a similar point of view around the 1960s? As Weiner (1994), Collins (1986), and others have emphasized, the mere accumulation of evidence surely played a major role. The story of Kettlewell's melanic moths, for example, is usually told as a story about the validation of theory by evidence. All of the theoretical machinery needed to describe evolutionary change on the scale of decades, or even a few years, was in place by the 1930s. The idea that industrial pollution could explain the increasing frequency of melanic morphs of B. betularia observed in the late 19th century was afoot in the 1920s.[87] The narrative perpetuated by historians and scientists about industrial melanism (Grant 2012, Rudge, 2006, Hooper 2002) is that Bernard Kettlewell's observations of differential predation by birds clinched the deal by providing empirical support for propositions generated by theory.

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[87] Haldane (1924) used calculations based on models from theoretical population genetics to show that the rapid increase in melanic forms could, in principle, be explained by natural selection.

Similarly, in Jonathan Weiner's (1994) Pullitzer prize-winning book, *Beak of the Finch*, we find evolutionary ecologists Peter and Rosemary Grant on an island in the Galapagos diligently documenting the evolutionary changes in the beaks of finches about which Darwin theorized, but did not measure. In discussing the significance of direct evidence for natural selection in natural populations, Weiner (1994, p. 8) quotes geneticist Raymond Pearl's forward to G. F. Gausse's (1934) *The Struggle for Existence*:

> If ever an idea cried and begged for experimental testing and development, surely it was this one. Yet the whole array of experimental and statistical attempts in all these years to produce some significant new evidence about the nature and consequences of the struggle for existence is pitifully meager. … And there is surely something comic in the spectacle of laboratories overtly embarking upon the experimental study of evolution and carefully thereafter avoiding any direct and purposeful attack upon a pertinent problem, the fundamental importance of which Darwin surely established. (Pearl 1934).

What made the work by Kettlewell, Bradshaw, and the Grants heroic was, from this perspective, their successful attempts to demonstrate the efficacy of natural selection in real time.

In the foregoing analysis of Bradshaw's research, however, we can see that the generation of new evidence is only one part of a much more complex story. The transition from Turesson's genecology of the 1920s to Bradshaw's ecological genetics in the 1960s involved a long sequence of methodological and conceptual adjustments. By the middle of the 1960s Bradshaw and his students had produced far more than a new body of evidence:

they had developed a new configuration of questions, hypotheses, materials, and methods that made it *possible* to generate evidence for rapid adaptive evolution. What made Bradshaw's work influential was not that it proved Darwin right, but that it showed *how* Darwin's theory (and it subsequent refinements) could be investigated in natural populations. The innovation of Bradshaw's research was not merely a set of superficially radical claims pertaining to evolutionary theory, but rather a new configuration of materials, techniques, questions, and epistemic norms that moved rapid adaptive evolution in natural populations into the realm of the tangible and investigable.

Among the diverse materials and informants upon which the conclusions of this dissertation are based, the single most important source of insight into Bradshaw's investigative pathway were the procedural notes, raw data, and hand-calculated statistical analyses contained in Bradshaw's research notebooks. Those notebooks provide an unparalleled window not only into Bradshaw's investigative practices, but also the evolving ways in which he conceptualized his research problems. This kind of research will require a radically different set of skills and tools as historians of science turn their gaze toward the latter half of the 20th century and the early decades of the 21st. Within a few decades of Bradshaw's move to Liverpool, computer technology had become an integral part of research across most (if not all) biological fields. In related research projects, I have interviewed ecologists whose only record of the data from their dissertation research is a set of magnetic tapes. Today, most research data are stored in large databases on institutional servers or personal harddrives. High-throughput technology in both the laboratory and in field research, and the rapidly declining cost of data storage, has resulted in an explosion of

data production. In response to this "data deluge" (Economist 2010), computational analysis has taken center stage in the biological sciences. The ability of historians of science to critically analyze biological research will soon depend on their competence to operate in that big-data computational environment. The necessary skillset will go well beyond the ability to operate consumer software: advanced training in computer programming, database architecture, and statistical modeling will be essential to interrogate, interpret, and analyze scientific practice. Two investigations that extend this disseration using computational methods—one involving the evolution of the Ecological Genetics Group, and another focused on patterns of collaboration among genecologists—are now underway.

Bradshaw's research did not occur in a vacuum and, as I have shown in the foregoing chapters, represented a series of moments along a much longer thread connecting Gregorian genecology with the rise of ecological genetics. This dissertation gestures toward the enormous scope for investigating the role of research styles and traditions in the development of 20th-century evolutionary biology. Until recently, much of the historiography of evolutionary biology during this period has focused on the disciplinary and theoretical implications of the Modern Evolutionary Synthesis. Over the past decade, however, historians have increasingly constrained the generality of the Synthesis narrative by emphasizing the variety of investigative traditions that persisted within evolutionary biology into the second half of the 20th century (e.g., in Cain and Ruse 2009). I have argued that the investigative and epistemic practices developed by genecologists working at the SPBS and WPBS constituted a distinctive research style, with substantial effects on the material and theoretical parameters of research conducted by its practitioners. The tight

coupling of that agro-genecological community of researchers and the development of the

Ecological Genetics Group over its first two decades of existence suggests that

this style may have continued to exert an influence well beyond the 1960s. This dissertation

is a starting-point for a broader investigation into the causes, contexts, and consequences of

the research styles and traditions that contributed to 20th-century evolutionary ecology.

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APPENDIX A

PRELIMINARY ANALYSIS OF EGG ATTENDANCE, 1956–1975

In this appendix I briefly describe several quantitative methods that I am developing to address questions about the evolution and diversification of the Ecological Genetics Group between 1956 and the present. Quanitative data about EGG attendance is only available for some of the early years of the group's history, but nevertheless paints an intriguing picture of the group's early growth and diversification. The results described here are preliminary, and suggests that there is substantial scope for a more comprehensive study.

A.1. Institutional diversity.

I used the Shannon index of diversity, *H*, to estimate the diversity of represented institutions at EGG meetings for each year (Eq. A.1). *H* is a measure of -diversity in ecology, and reflects both the total number of species in a habitat as well as the relative representation of those species. A habitat with a large number of species of similar abundance will have higher values of *H*, while those with a small number of species, or with widely varying abundance, will lower values of *H*. In the context of an institutional analysis, lower values of *H* should indicate cases in which the meetings were dominated by one or a few institutions. Indeed, the low values of *H* prior to 1960 reflect the fact that only WPBS, SPBS, and Bangor were represented.

$$H = -\sum_{i=1}^{s} pi \ \ln p_i \qquad \text{(Eq. A.1)}$$

Figure A.1 shows *H* for the period 1956–1975. Institutional diversity jumped in 1960, at the Shrewsbury meeting, and increased in a roughly linear fashion thereafter. Much of the changes in both recruitment (Figure 4.3.2) and diversity (Figure A.1) reflected in the data for in 1964 were due to changes at the 1961 meeting, as described in section 4.5.
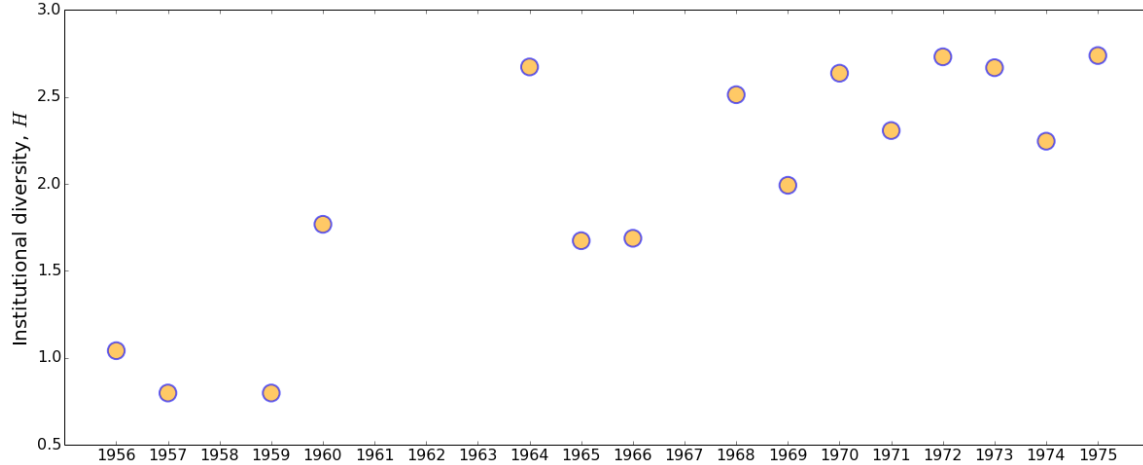
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Figure A.1. Diversity of institutional representation at EGG meetings, 1956–1975. Shannon's *H* metric of diversity reflects both the number of different (in this case) institutions represented, as well as the relative proportions of attendees from those institutions. Institutional diversity peaked in 1964, and remained relatively high through the end of the study period.

A.2. Taxonomic diversity

The meetings in 1964–1966 were characterized by an increase in the taxonomic diversity of attendees, indicated by the attendance of researchers who focused on taxa that were highly dissimilar to those of previous attendees (Figure A.4). For each attendee, I identified the taxon or taxa on which their Ph.D. research focused. I then pooled the focal taxa of the attendees of each meeting. For each year, I calculated the taxonomic distinctness (of each taxon represented in that year in comparison both to the taxa in previous years (Figure A.4A) and in the same year (Figure A.4B).

The concept of taxonomic distinctness (δ_a) used here is based on a measure of beta-diversity proposed by Izsak and Price (2001), the taxonomic similarity index (Δ_s). Taxonomic similarity is defined as:

$$\Delta_s = 1 - \frac{TD}{L-1} \qquad \text{(Eq. A.2)}$$

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Taxonomic distance (*TD*) is based on the "shortest path length", , between two species *a*

and *b* in a composite graph of their lineages. For example, the lineages of *Agrostis tenuis* and

Agrostis stolonifera both belong to the same. In a system with ranks species, genus, family, and

order, their lineages would intersect at the second rank (genus). Given two sets of taxa, *A*

and *B*, perhaps representing the taxa present in two adjacent habitats, taxonomic distance is

calculated (Eq. A.3) by summing the minimum shortest path length between each taxon *a* in

A in each taxon *b* in *B*, as well as the reverse comparison. The resulting value is normalized

by the size of taxa-sets *A* and *B*.

$$TD = \frac{\sum_{a \in A} \min (w_{a \to b}) + \sum_{b \in B} \min (w_{b \to a})}{n_A + n_B} \tag{Eq. A.3}$$

L (in Eq. A.2) is the number of taxonomic ranks used in the calculation of *TD*. So for the

system described above (species, genus, family, order), .

Taxonomic distinctness indicates the pecularity of a taxon given some other set of

taxa. In contrast to taxonomid similarity (Δ_s), which compared two sets of taxa, taxonomic

distinctness is a comparison between a single taxon and a set of taxa. Taxonomic distinctness

uses the shortest path length calculation from Eq. A.3. Given the taxon *a* and a set of taxa *B*,

$$\delta_a = \min_{b \in B} \Omega_{a,b} \tag{Eq. A.4}$$

$$\Omega_{a,b} = \left[\frac{w_{a \to b}}{L}\right]^3 \tag{Eq. A.5}$$

Cubing the normalized path length in Eqation A.5 serves to place greater weight on higher

taxonomic ranks. Figure A.3 shows the system used to $\Omega_{a,b}$ for pairs of taxa sharing a given

rank.

A.3. Institutional context

Figure A.5 provides a visual representation of taxonomic differences across Ph.D.

institutions of EGG attendees. Nodes represent institutions represented by attendees of

EGG meetings from 1956 through 1975. The size of each node corresponds to the total

number of attendees who received Ph.D.s from those institutions, and the directed edges

(lines and arrows) indicate the movement of those scientists to research positions at other

institutions following the completion of their degree. For each institution, I calculated the

taxonomic distinctness of a reference species, sweet vernal grass (*Anthoxanthum odoratum*), in

relation to the focal organisms of Ph.D. recipients from that institution. Bluer colors indicate

lower δ_a, and redder colors indiate δ_a. Unsurprisingly, Oxford, Manchester, Nottingham,

Stirling, Newcastle, and Swansea had some of the highest values of taxonomic distinctness

for *A. odoratum*, reflecting the tendency of researchers from those insitutions to work on

non-plant organisms. Attendees from Aberystwyth, Bangor, Durham, and Leeds, however,

were much more focused on plants, especially the Gramineae.

I repeated this procedure across all taxa in the dataset (i.e. using each taxon in turn as

the reference taxon, *a*, to calculate δ_a), and then calculated the average difference between

values at each institution compared to a reference institution (University of Wales,

Aberystwyth). The grouping of institutions depicted in Figure A.5 is also apparent in that

analysis (Figure A.6). I then calculated pair-wise differences in all-taxa distinctness for all

institutions, and used the centroid agglomerative clustering algorithm (Day 1984) to generate

hierarchical linkages among the institutions. Given a cutoff threshold of 0.5 (i.e. a ratio of

linkage heights between versus within clusters of 2:1), there appear to be three major

coherent institutional groups (Figure A.7). Further analysis is required to interpret the
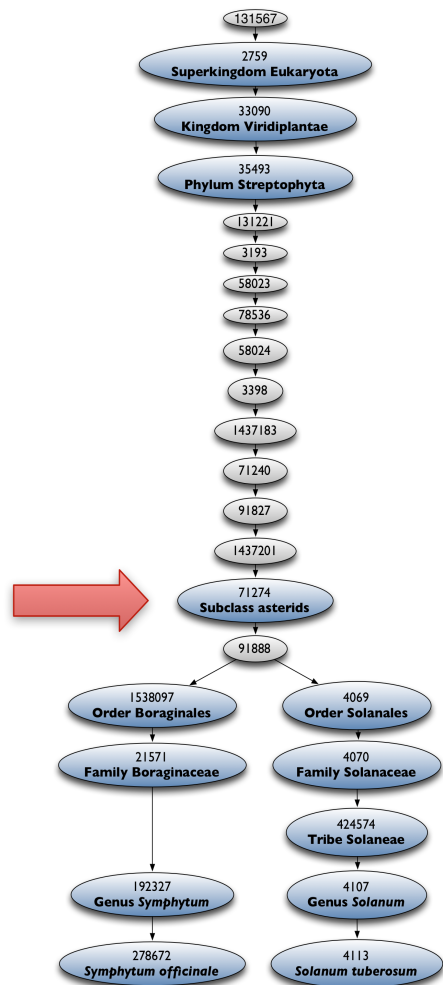
meaning and significance of those groupings.

Figure A.2. Finding the shortest path length between two taxa based on the lowest shared taxonomic rank. In this example, *Solanum tuberosum* and *Symphytum officinale* share the rank of subclass.
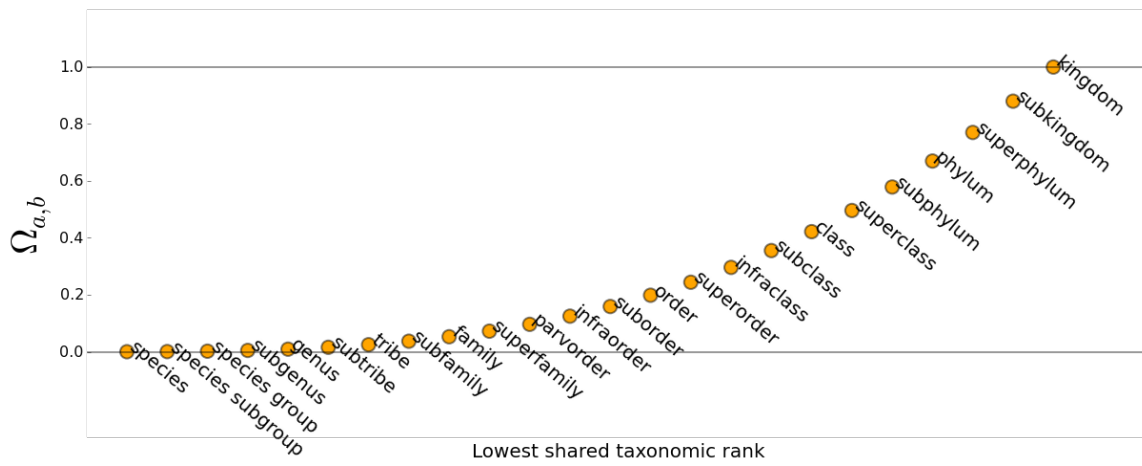
Figure A.3. Values of $\Omega_{a,b}$ for each of the taxonomic ranks used to calculate taxonomic distinctness in figure 4.3.4.
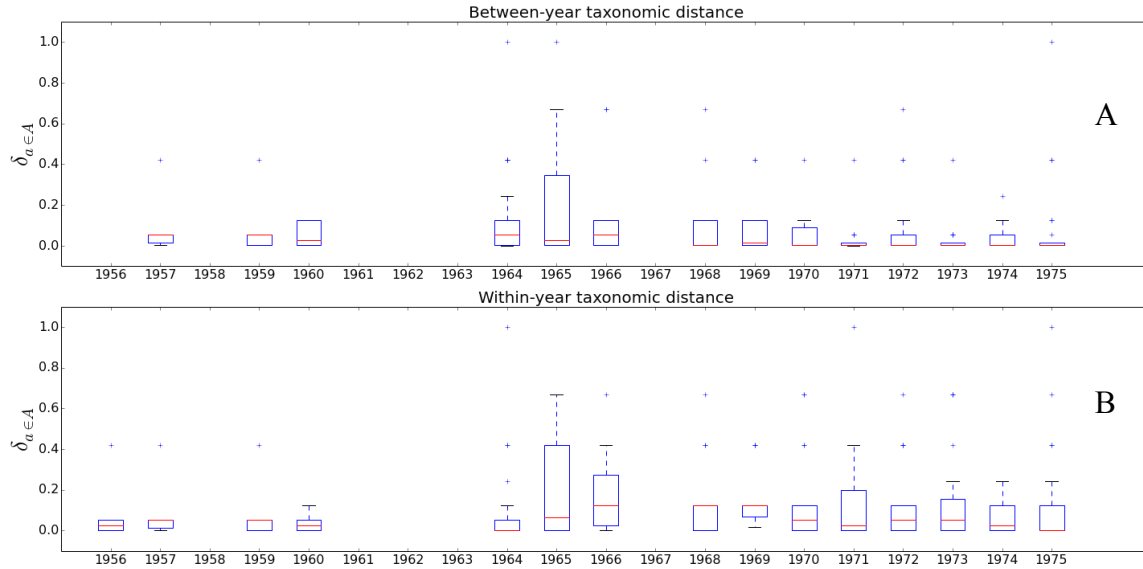
Figure A.4.. Taxonomic diversity of EGG meeting attendees (A) between years and (B) within years. $\delta_{a \in A}$ measures the taxonomic dissimilarity of taxon **a** in the set of taxa A with respect to some other set of taxa, B. See equation 4.3.2. In between-year comparisons (A), taxa-set B is all of the taxa represented in preceeding meetings. In within-year comparisons (B), taxa-set B is all of the taxa represented in that year, excluding **a**. Box and whisker plots show the median (red lines), lower and upper quartiles (blue boxes), range (whiskers), and outliers (points). Data are missing for 1958, 1961–1963, and 1967.
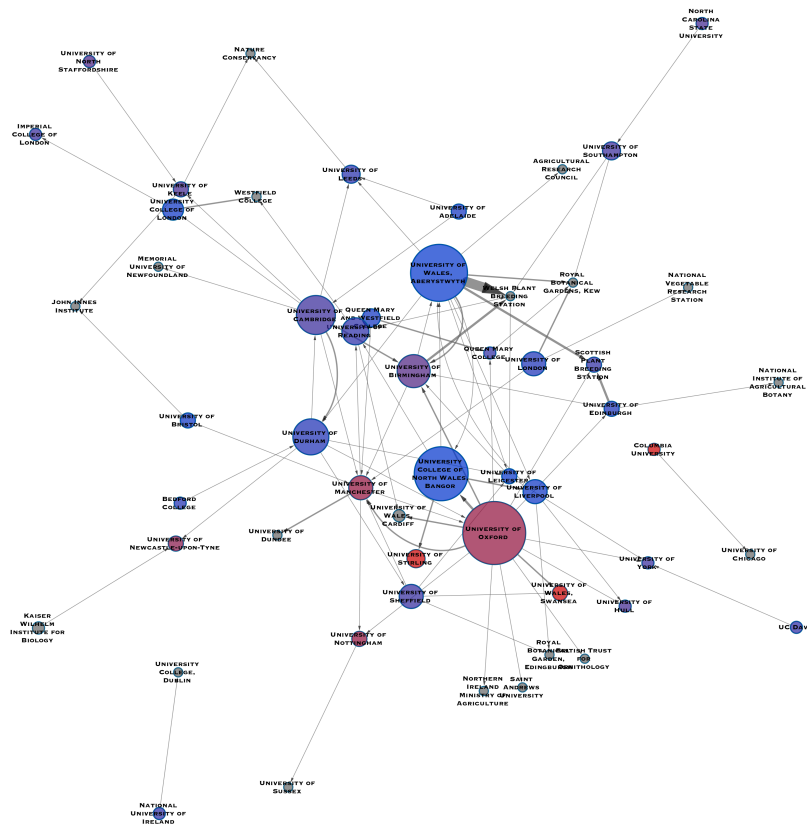
Figure A.5. Patterns of circulation in employment, PhD to post-doctoral positions, for EGG attendees 1956–1975.
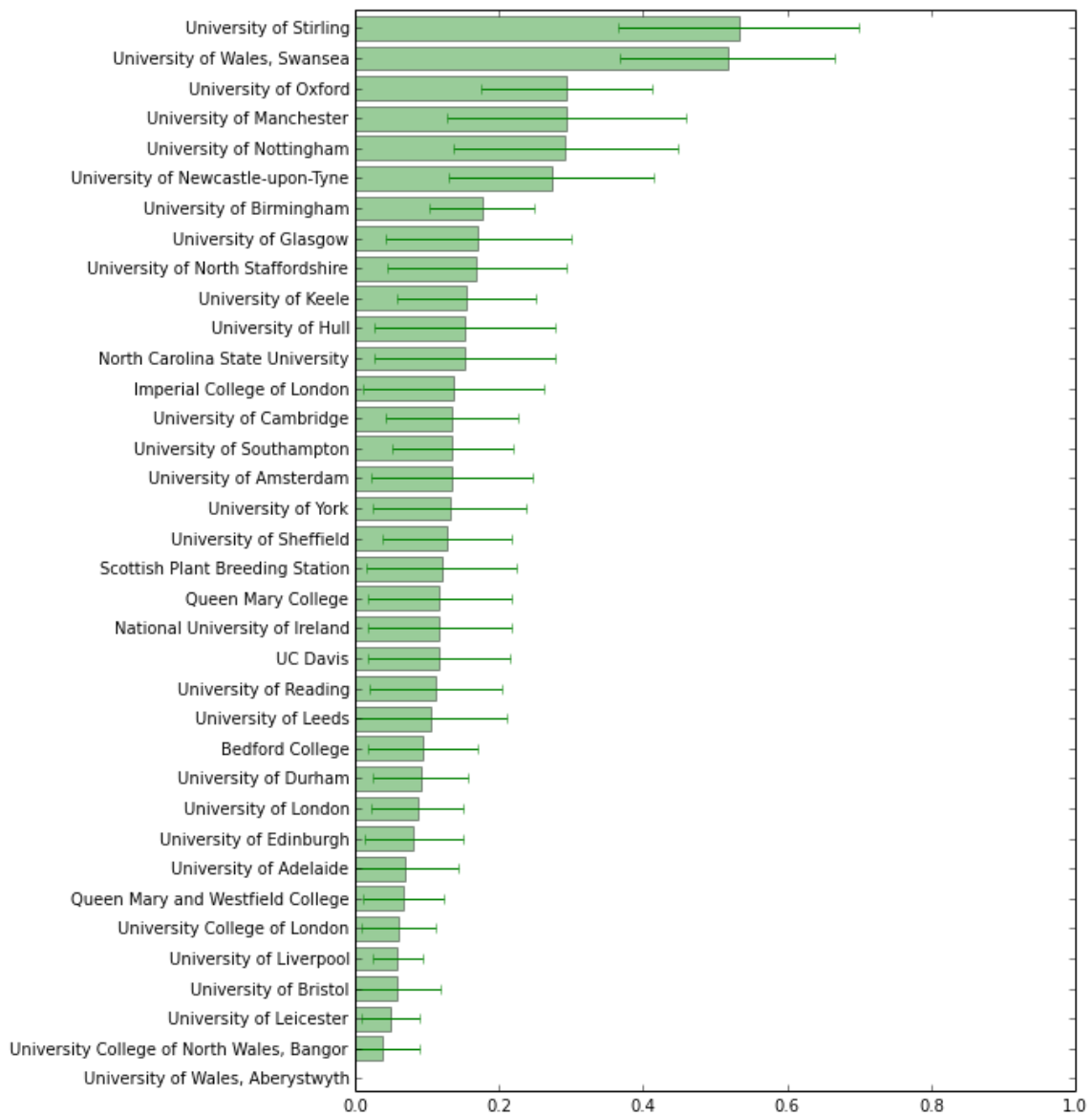
Figure A.6. Mean taxonomic distinctness values for each instution represented at EGG meetings, 1956–1975. University of Wales, Aberystwyth, is used as a reference.
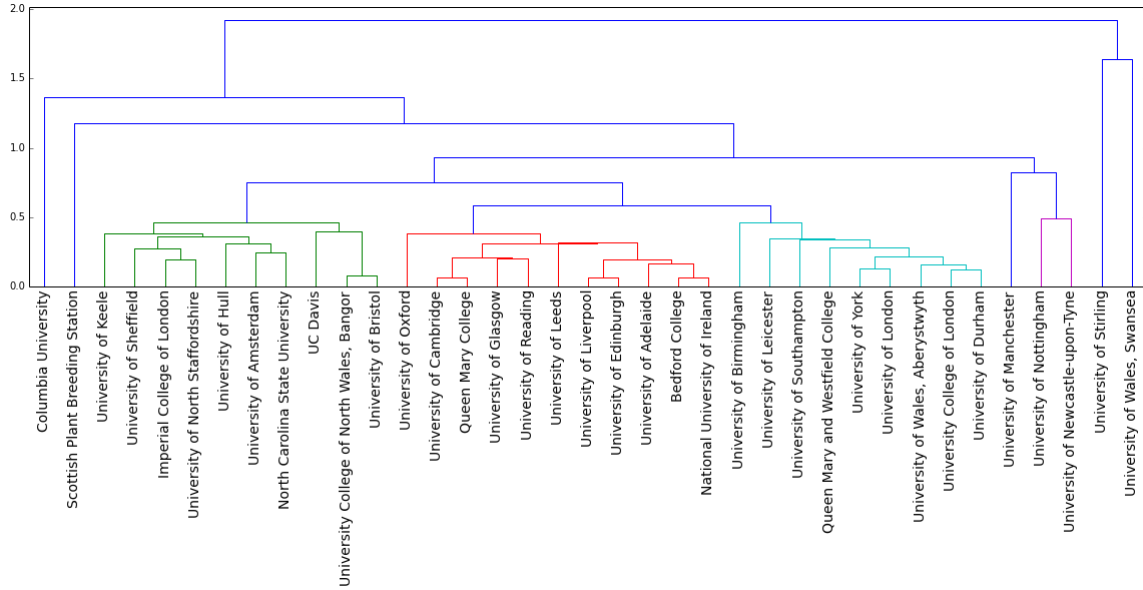
Figure A.7. Clustering of institutions represted at EGG meetings (1956–1975) based on average pair-wise taxonomic distinctness of focal organisms in attendee dissertations. Generated using the centroid agglomerative clustering algorithm (Day 1984) and a cutoff threshold of 0.5.