Beginnings of Wetland Science in Britain: Agnes Arber and William H. Pearsall

Arnold van der Valk, Professor Emeritus Ecology, Evolution, and Organismic Biology Iowa State University
Ames, IA 50011
valk@iastate.edu

ABSTRACT

Agnes Arber (1879-1960) and William H. Pearsall (1891-1964) were two of England's most influential antecedent wetland scientists. Arber was a plant anatomist specializing in monocotyledons, whose only major contribution to wetland science was her 1920 book, *Water Plants*. It was the first compendium of information on wetland plants in English and summarized the literature on their life histories, anatomies, ecologies, and evolution. It remained the standard reference on wetland plants for decades after its publication. William Pearsall began studying the ecology of wetland plants in the lakes of the English Lake District as a young man. This early research (1913-1920), which he did with the help of his school-teacher father, identified the environmental factors (substrate type, siltation rates, maximum light penetration, wave action, etc.) that determined the distribution of wetland plants and changes in the lake basins over time. In the late 1930s, Pearsall pioneered measuring electrical potential (redox) in soils to characterize their chemical status (oxidizing or reducing). He documented that soil electrical potentials became more negative as soils flooded and increased in organic matter. Pearsall also played a major role in the establishment (1929) and initial research program (Honorary Director, 1931-1937) of the Freshwater Biological Association, Britain's first research organization dedicated to studying aquatic systems.

INTRODUCTION

By the beginning of the 20th Century, there had been studies on the biology and evolution and, to a lesser extent, ecology of wetland plants in the British Isles. However, the publication by Agnes Arber of *Water Plants* in 1920 and a series of papers by William H. Pearsall, beginning in 1917, on the distribution of wetland plants and vegetation in the lakes of the English Lake District were major milestones in the development of wetland science, not only in England but globally. Arber, a plant anatomist by training, earned a doctorate from University College London and briefly held an academic position there. She moved to Cambridge to be with her husband but could not obtain a permanent academic position at Cambridge University. Water Plants was her single significant publication in wetland science. By contrast, William Pearsall began his studies of the wetland vegetation of English lakes in 1913 with the help of his father. His studies eventually earned him a master's degree, a doctorate, and a university position. Pearsall had a long and distinguished academic career at several British universities. His field studies set a new standard for research on wetland plants and vegetation and the environmental factors controlling their distribution. In short, Arber was only briefly an antecedent wetland scientist, while Pearsall was one of the most important and influential of all antecedent wetland scientists.

In what follows, I briefly outline the scientific careers of Arber and Pearsall, emphasizing their most significant contributions to the development of wetland science. In both cases, but especially in Arber's, they made major scientific contributions outside of wetland science that I have ignored. Fortunately, because they were both elected Fellows of the Royal Society, there are excellent biographies of Arber (Thomas 1960) and Pearsall (Clapham 1971) that provide a complete account of their scientific achievements. As a woman, Arber could not obtain a postgraduate degree at Cambridge University and later, when she was a renowned botanist, was denied research space at Cambridge University. Her struggles as a woman trying to establish a scientific career in the first half of the 20th Century have made her a feminist icon. For an examination of Arber's life and career from a feminist prespective, see Packer (1997) and Schmid (2001).

AGNES ARBER (1879-1960)

Figure 1. Agnes Arber in 1916. (Courtesy of Wikipedia)

Agnes Arber (née Robertson) (Figure 1) was an internationally renowned plant morphologist/anatomist, historian of botany, and philosopher of biology. She was born in London in 1879 and died in Cambridge in 1960. From 1887 to 1897, she attended the progressive North London Collegiate School for Girls. From 1897 to 1899, she studied at University College London, receiving a B.Sc. From 1899 to 1902, Arber was a student at Newnham College, Cambridge University. Although she was an outstanding student, she did not receive a degree. Cambridge, at this time, would not award degrees to women. After her time at Cambridge, Arber returned to London and worked as a research assistant (1902-03) with Ethel Sargant, an important plant anatomist, in Sargant's home laboratory. From

1903 to 1909, Arber was a graduate student (D. Sc, 1905), teaching assistant, and lecturer in Botany at University College London.

After she married Edward Alexander Newell Arber, she resigned from her position at University College London and moved to Cambridge to be with him. E. A. N. Arber also had gone to University College London but had taken a position as a paleobotanist at Cambridge University. Agnes Arber spent the rest of her life in Cambridge. After moving to Cambridge, she published a book on herbals (Arber 1912). From 1914 to 1927, Arber did her research at the Balfour Biological Laboratory for Women, run by Newnham College. When Newnham College could no longer afford to keep Balfour Laboratory open, the College had to sell the building housing it. Despite an effort by the head of Newnham College to find Arber space for her research at Cambridge, Arber was not provided laboratory space. However, Newnham College allowed Arber to take her laboratory equipment with her to set up a laboratory in her home. She worked at home from 1927 to 1959. Nevertheless, she did not become a recluse and continued to attend scientific meetings.

Arber was nominated in 1921 for the presidency of Section K (Botany) of the British Association for the Advancement of Science, but her male colleagues opposed her nomination (Packer 1997). However, her contributions to science were widely recognized and resulted in her being elected in 1946 as a fellow of the Royal Society, the third woman to receive this honor. For more detailed accounts of Arber's life and work, see Thomas (1960), Packer (1997), and Schmid (2001).

Introduction to Botany – Student of Ethel Sargant

Agnes Arber first met Ethel Sargant when she was a pupil at North London Collegiate School for Girls. Ethel Sargant (1863-1918) was a botanist whose research focused on the vascular anatomy of seedlings. According to Arber (1919a), "From 1881 to 1885 she [Sargant] studied natural science at Girton College, Cambridge, but nearly all her subsequent work was carried out at home, where domestic ties [her aging mother and mentally handicapped sister] involved continuous demands upon her time and vitality, and often interrupted her own private pursuits for long periods …. The conditions of her life made any professional undertaking -- in the sense of a teaching post -- impossible for her, but she was far from regretting this disability, since she was convinced that lecturing and demonstrating would, in her case, have paralysed the faculty for original work." Despite her "domestic ties", Sargant had an exceptional and influential research career that in 1903 produced a major monograph: "A theory of the origin of monocotyledons, founded on the structure of their seedlings" (Sargant 1903). Sargant invited Arber to work in her home laboratory between school and college and during Arber's long vacation from Cambridge. Sargant and Arber (1915) published a major paper on "The morphology of the embryo and seedling in the Graminea." Working with Sargant, Arber learned the technique for making anatomical slides of plants, how to interpret them, and, more importantly, how to do research.

Like her mentor, Arber's scientific research focused primarily on the morphology and anatomy of monocotyledons. Flowering plants or angiosperms have been traditionally divided into two major groups, monocotyledons and dicotyledons. As their name implies, one of the defining characteristics of monocotyledons is seeds that contain a single embryonic leaf or cotyledon. Some of the most important and common species of monocotyledons are in the grass family, but there are also a large number of families of monocotyledons among aquatic plants (Arber 1919b, 1920). Arber's earlier studies concerned the development and internal anatomy of leaves and other vegetative organs of monocotyledons. Establishing the origin of monocotyledons was a major goal of her research program. Arber would eventually publish three books that summarized her research: *Water Plants: A Study of Aquatic Angiosperms* (Arber 1920), *Monocotyledons: A Morphological Study* (Arber 1925), and *The Gramineae: A Study of Cereal, Bamboo, and Grass* (Arber 1934). It is the first of these books, *Water Plants*, that had a significant impact on the development of wetland science.

Publication of *Water Plants*

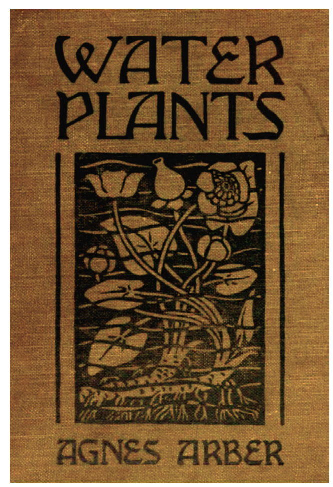

Figure 2. Cover of *Water Plants*.

Arber's *Water Plants* (Figure 2), dedicated to her recently deceased husband, is a major update and expansion of Heinrich Schenck's (1886) *Die Biologie der Wassergewächse*. Schenck compiled in his monograph all the information available on the anatomical and morphological adaptations that allowed plants to live in aquatic systems (van der Valk 2017). Arber (1920) updates Schenck but does so in an evolutionary framework. In the Preface to *Water Plants*, Arber states: "I approached the study of Water Plants with the hope that the consideration of this limited group might impart some degree of precision to my own misty ideas of evolutionary processes." However, the book deals with much more than the evolution of hydrophytes. Like Schenck's book, *Water Plants* is a valuable compendium of information on aquatic plants that summarizes what was known about their biology, ecology, and evolution. In 1919, Arber published several papers on aquatic plants (Arber 1919b, c, and d) that became the bases for chapters in *Water Plants*.

Water Plants is divided into four sections. Part I covers

"WATER PLANTS AS A BIOLOGICAL GROUP, WITH A CONSIDERATION OF CERTAIN TYPICAL LIFE-HISTORIES." It contains ten chapters, all of which, except the first, on the classification of water plants, summarize what is known about the life history of one or more representative taxa of aquatic plants. Part II deals with "THE VEGETATIVE AND REPRODUCTIVE ORGANS OF WATER PLANTS, CONSIDERED GENERALLY." This section has chapters on leaves, stems, roots, flowers, and fruits, as well as on vegetative reproduction. Part III concerns "THE PHYSIOLOGICAL CONDITIONS OF PLANT LIFE IN WATER." It has only four chapters. Three chapters discuss gas exchange, nutrient uptake, and physical factors. The fourth is an overview of the ecology of water plants. Part IV concerns "THE STUDY OF WATER PLANTS FROM THE PHYLOGENETIC AND EVOLUTIONARY STANDPOINTS." The first chapter in this section is on the dispersal and distribution of water plants. The remaining four chapters are concerned with the systematic distribution of water plants, the aquatic origin of monocotyledons, natural selection and water plants, and water plants and the law of loss in evolution.

Since the stated purpose of this book is to elucidate evolutionary processes, Arber's discussion of this topic is of particular interest. One major evolutionary question that Arber addressed is the origin of aquatic plants. There were two competing theories at the time: were they escapees from terrestrial environments or hardy pioneers of the plant world? Arber's answer: "… the assumption [is] that the adoption of an aquatic life is a device by which a poorly equipped species may escape from the competition of its more favoured compeers, saving itself from extinction by retirement into a quiet back-water of existence. In other words, water life is regarded as a refuge for the destitute among plants. The present writer, having begun the study of aquatics ten years ago with a full conviction of the truth of this picturesque theory, has gradually and reluctantly been forced to the conclusion that there is no sound evidence in its favour. On the hypothesis in question, water plants are more or less comparable with the remnant of a defeated race among mankind, which preserves its existence by retreating into some forbidding and inaccessible region, into which its conquerors have little temptation to pursue it. But this analogy is probably quite misleading; it would perhaps be more illuminating to compare water plants with the pioneers who are to be found leading hard and difficult lives in barbaric regions on the frontiers of civilisation not forced thereto by failure to 'make good' in the excessive competition prevailing in regions more anciently inhabited, but impelled to the frontiersman's life by a natural, inborn affinity for the adventurous conditions which it offers. In the same way, water plants appear to the present writer to have adopted this mode of life, not as a last resource, but because it happened to suit their particular constitution and character. There is little doubt that, after they had once entered upon an aquatic career, they must have evolved along lines which gradually harmonised them more and more completely with their surroundings, but the initial step or steps, which led to the adoption of the water habit, must have been due to an innate affinity for the environment, rather than to the negative quality of incapacity for success in terrestrial life; to pursue our metaphor the man, who fails in the struggle for existence at home, is not of the type that makes the successful colonist."

Arber's *Water Plants*, like Schenck's Die Biologie der Wassergewächse before it, raised the visibility of aquatic plants and aquatic systems in the first half of the 20th Century. It also made the literature on them, much of it in German, easily available to non-German speakers and stimulated further work on aquatic plants and aquatic systems. According to Google Scholar, *Water Plants* has been cited nearly 1,000 times, making it a classic in the history of wetland science. Schenck's *Die Biologie der Wassergewächse* has been cited only 36 times. It is by far Arber's most frequently cited work. There would not be an update for more than 45 years, C. D. Sculthorpe's (1967) *The Biology of Aquatic Vascular Plants*.

WILLIAM HAROLD PEARSALL (1891-1964)

Although William H. Pearsall's early papers (1917-1918) are only cited in a footnote in Arber's *Water Plants*, his ecological studies of aquatic plants and vegetation in the 1910s, 1920s, and 1930s ushered in a new era for wetland science in Britain. According to G. E. Fogg (1979), "The beginnings of organized freshwater biology in Britain may be seen in the work of W. H. Pearsall on the aquatic plants of the English Lakes."

Pearsall (Figure 3) was born in 1891 at Stourbridge, near Birmingham in the West Midlands of England. His father was a schoolteacher and a keen amateur naturalist interested in the English Lakes. Pearsall senior and junior spent their summer holidays in the Lake District collecting aquatic plants. Pearsall senior was a self-taught expert on several genera of aquatic plants (pondweeds, starworts, and aquatic buttercups). William Pearsall attended his father's school until 1905 and then Ulverston Grammar School. In 1909, he was admitted to Victoria University of Manchester and gradu-

Figure 3. William H. Pearsall in 1941. (Courtesy of the National Portrait Gallery)

ated in 1913 with a degree in Botany. Upon graduation from Victoria University, he was awarded a University Graduate Scholarship. With the help of his father, he then began a systematic survey of the distribution of aquatic plants in the 11 English Lakes. The objective of this study was to relate their distribution to substrate characteristics, water transparency, and water chemistry. In 1914, he surveyed the distribution of aquatic plants in Esthwaite Water, which resulted in the publication of his two-part paper "The aquatic and marsh vegetation of Esthwaite Water" (Pearsall 1917-1918). Based on this work, he was awarded an M.Sc. in 1915. World War I interrupted his academic career, and in 1916 he joined the Royal Artillery and was sent to France. Pearsall had permanent hearing loss when he returned to England in 1919. That same year he became an Assistant Lecturer in Botany at the University of Leeds. In 1920, he was awarded a D.Sc. from Manchester University for his work on the wetland vegetation of the English Lakes, and in 1922 he was promoted to Reader in Botany at Leeds. He moved from Leeds to Sheffield in 1938 to become Chair of Botany. Pearsall's final academic position was the prestigious Quain Chair of Botany at University College London from 1944 until his retirement in 1957. Pearsall joined the British Ecological Society soon after its foundation and became its president in 1936. From 1937 to 1947, he was Editor of the Society's *Journal of Ecology*. In 1940 he was elected a Fellow of the Royal Society, six years before Agnes Arber. W. H. Pearsall died in 1964.

Pearsall had a long, distinguished, and varied career as a researcher, but during its second half, his research had little or nothing to do with wetland science, e.g., his work on primary production, protein chemistry, and Serengeti National Park. To the development of wetland science, Pearsall made three important contributions: (1) his detailed studies of the distribution of wetland plants and vegetation in the lakes of the English Lake District, (2) his pioneering studies of oxidation-reduction (redox) potentials in wetland soils, and (3) his role in the establishment of the Freshwater Biological Association. For a complete account of William Harold Pearsall's life and scientific career, see Clapham (1971).

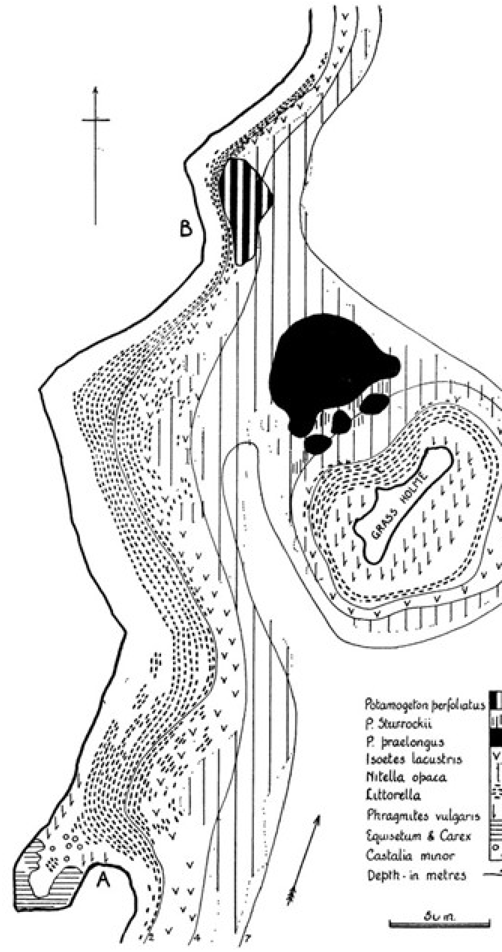

Figure 4. Map of Grassholme Island area along a small section of the western shore of Lake Windermere shows the relationship of *Potamogeton* spp. to shelter and to silting and the distribution of *Castalia minor* (*Nymphaea odorata* var. *minor*) and *Equisetum-Carex* reedswamp in a closed bay (lower left). Figure 10 from Pearsall (1920).

Studies of Wetland Vegetation of English Lakes

In his 1911 book *Types of British Vegetation* A. G. Tansley reported that "Comprehensive studies of aquatic vegetation … have not yet been carried out in this country." William Harold Pearsall would soon change this.

With his father's help, Pearsall spent seven years, 1913-1920, studying the vegetation of 11 lakes in the English Lake District in northwest England. His overarching goal was to identify the factors controlling the distribution of wetland plants in the lakes. His first papers were on the vegetation of Esthwaite (Pearsall 1917-1918). They focused on the physical features of the lake and how these affected the distribution of its submerged and emergent communities (Figure 4). Esthwaite has a winding shoreline that creates a wide range of water depths, wind and wave exposures, sedimentation rates, and sediment types. It also had a large number of different plant assemblages. Pearsall's decision to concentrate initially on Esthwaite enabled him to become familiar with its various plant assemblages and the environmental conditions where they were found.

'The development of vegetation in the English Lakes, considered in relation to the general evolution of glacial lakes and rock basins' (Pearsall 1921) summarized his seven years of research in the Lake District. Among the features of each lake surveyed were the percentage of the lake shores, down to 30 ft, that were rocky; the percentage of a lake's watershed (drainage basin) cultivated or cultivatable; the transparency of the water; and chemical characteristics of a lake's sediments and water. Pearsall correlated environmental variables to the distribution of vegetation communities in the lakes, including the types of phytoplankton. He noted that the whole of the Lake District had been glaciated during the Pleistocene, and the retreat of the glaciers resulted in many rock basins and that all the lakes he studied originated in these rock basins. However, with time the lake basins diverged significantly. In the 1920s, the percentage of rocky shores around the lakes ranged from 12% for Esthwaite to 73% for Wastwater and cultivatable land in a basin from 5.2% for Wastwater to 45.4% for Esthwaite. Because the water of the silted lakes carries more fine material in suspension, the rockier the basin, the more transparent the water. Another factor that contributed to siltation in these lakes was softer rocks along the shores in some lake basins. Pearsall recognized that lakes and lake basins become modified as they age and that the lakes in the Lake District illustrated the processes that controlled lake development.

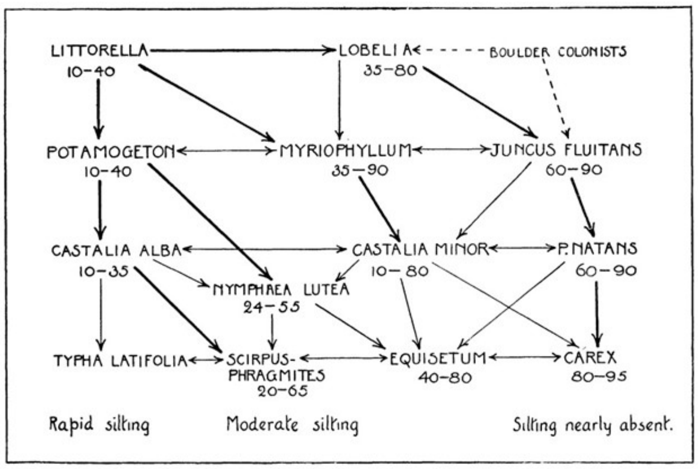

Figure 5. Succession sequences of shallow water communities in rapid, moderate, and low silting areas. The numbers below each community are the percent organic content of the soil. Figure 13 from Pearsall (1920).

From his Esthwaite and subsequent lake studies, Pearsall (1920, 1921) concluded that the distribution and succession of wetland vegetation was a function of rates of silt deposition (Figure 5) and the physical and correlated chemical properties of the accumulated sediments. The various plant assemblages were found in more or less narrow zones parallel to the shoreline at differing depths. In the case of submerged aquatics, Pearsall believed that their zonation pattern was not the result of differences in their light requirements per se but due to differences in the rate and type of siltation in different zones. His data demonstrated that light penetration depths varied from lake to lake (Figure 6), and as expected, light penetrated furthest in Wastwater and least in Esthwaite. Aquatic plants are found in depths up to 7.7 meters in Wastwater but only to 4.1 meters in Esthwaite.

Pearsall was not the first to study the vegetation of lakes (for example, see Tansley 1911 and Chapter 23 in Arber 1920). However, his studies were far more detailed, sophisticated, and comprehensive than those of his predecessors, e.g., Guppy (1893) and West (1906, 1910). He set the standard for all subsequent wetland vegetation studies not only in Britain but around the world.

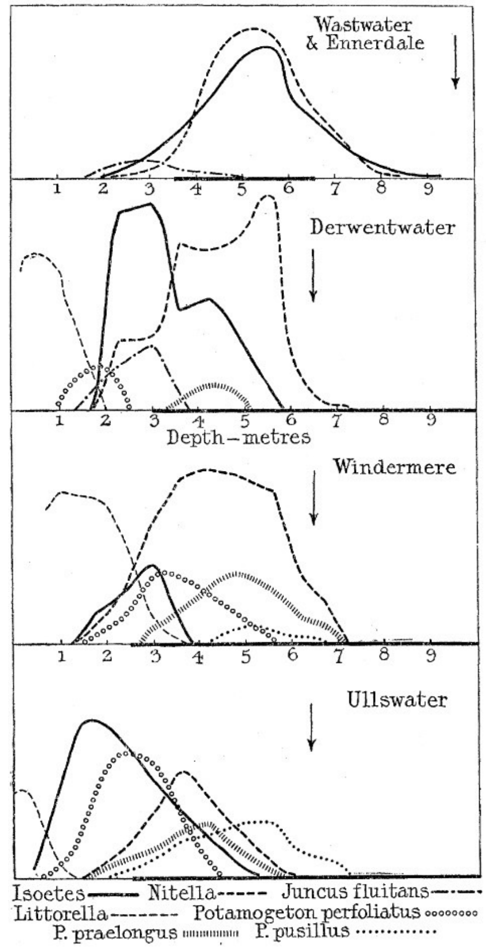

Figure 6. Depth distribution of characteristic species in the lakes of the English Lake District. The arrows show the light limit for vegetation in a lake. The thickened parts of the baseline of each panel indicate the depths in the lake that are normally silted. Figure 2 from Pearsall (1921).

Pioneering Reduction-Oxidation Potentials

Reduction-oxidation or redox is a chemical reaction in which electrons are gained or lost by a compound. A gain of electrons is a reduction, and a loss is an oxidation. Redox potential is a measurement of the potential for the transfer of electrons from one compound to another. In wetland soils, as organic matter decomposes, electrons and hydrogen ions are released. Under aerobic conditions, the electrons and hydrogen ions react with oxygen to form water. In other words, the organic matter loses electrons, i.e., it is oxidized, and oxygen gains them. This chemical reaction is aerobic respiration. It is the inverse of photosynthesis, and the energy fixed in organic matter by photosynthesis is released by aerobic and anaerobic respiration. The potential for the transfer of electrons between organic matter and oxygen has a voltage (V). This voltage is its redox potential (Eh). The redox potential for aerobic respiration under standard conditions (25° C and pH 7) is 0.82 or 820 mV, the highest voltage found in soils. When oxygen is depleted, the electrons released by organic matter decomposition are transferred to other terminal electron acceptors (nitrate, manganese oxide, ferric iron, sulfate, etc.), creating compounds other than water. For example, under anaerobic conditions, electrons can flow to sulfate, creating hydrogen sulfide. This reaction is called sulfate reduction, and the voltage associated with it is - 0.21 V, a much lower redox potential than that for aerobic respiration. Nitrate has a greater affinity for electrons than sulfate but less than oxygen. Suppose both nitrate and sulfate are present in anaerobic soils. In that case, electrons will preferentially flow to nitrate (Eh 043 V) and will not flow to sulfate (Eh -0.21) until all the nitrate has been converted to nitrogen gas. The reduction of nitrate is called denitrification. By the early 1930s, redox reactions had been studied by chemists under laboratory conditions. However, whether redox potentials could be measured in natural water or soils was unknown. Nor was the ecological significance of redox reactions understood.

In 1938, Pearsall published three papers entitled "The soil complex in relation to plant communities," Parts I, II, and III (Pearsall 1938a, b, c). In Part I, "Oxidation-reduction potentials in soils," Pearsall describes chemical theories that are the bases for redox measurements and a technique for measuring the electric potentials of soils. Chemists and biochemists had previously worked out the underlying theory and methodology but using oxidation-reduction potentials to characterize uncultivated soils had not been attempted. Pearsall measured soil electric potentials between a clean platinum electrode inserted into the soil and a calomel reference electrode (a substitute for a cumbersome hydrogen electrode) connected by a KCI-agar bridge. Electric potentials measured in different soils had to be adjusted to a common pH to make them comparable. Because the average pH of soils in northern England was 5, Pearsall adopted a standard pH of 5. This adjusted Eh was called Eh5.

After measuring soil potentials from many types of natural soils, Pearsall found that electric potentials decreased as their water content increased. Waterlogged soils typically had potentials below 200 mV. He also found that soils with potentials of 350 mV contained no detectable ferrous (reduced) iron, while those below 320 mV did. Pearsall concluded that pH-adjusted potentials between 320 and 350 mV marked a transition between oxidizing and reducing conditions: soils with Eh5s above 350 mV were oxidizing soils, and those with Eh5s below 320 mV were reducing soils. Pearsall's three 1938 papers demonstrated that methods developed in the physical sciences could be used to characterize the chemical environment of ecological systems. Although initially, there were difficulties with the field application of the methodology and in the interpretation of field measurements, these were soon resolved, and the method yielded reliable and interpretable results.

In 1939 Pearsall published a follow-up paper with C. H. Mortimer of the Freshwater Biological Association - "Oxidation-reduction potential in water-logged soils, natural waters and muds." It confirmed that "approximately stable reproducible potentials can be demonstrated in soils and muds …, and in natural waters at least in a zone between 250 and 350 mV at pH 5." Their studies also confirmed that products of oxidation (ferric iron, nitrate, sulfate) are found at higher adjusted potentials (350 mV or higher), while their reduced counterparts (ferrous iron, ammonia, sulfide) are present at potentials below 350 mV. With a simple experiment in which air or nitrogen was bubbled through a soil slurry, Pearsall and Mortimer demonstrated that in aquatic ecosystems, oxidation-reduction reactions were easily reversible (Figure 7).

Because redox reactions regulate the quantity and chemical nature of many dissolved substances in water and saturated soils, Pearsall's pioneering studies of the electrical potentials of soils and water were of great ecological significance. His studies ushered in a new era in wetland science, especially wetland biogeochemistry. Pearsall demonstrated that waterlogged soils are usually anaerobic and that a buildup of organic matter in wetland soils typically lowers redox potentials. Measuring redox in wetlands has become an essential tool in studying many aspects of wetland ecology, from the distribution of invertebrates to the design of treatment wetlands.

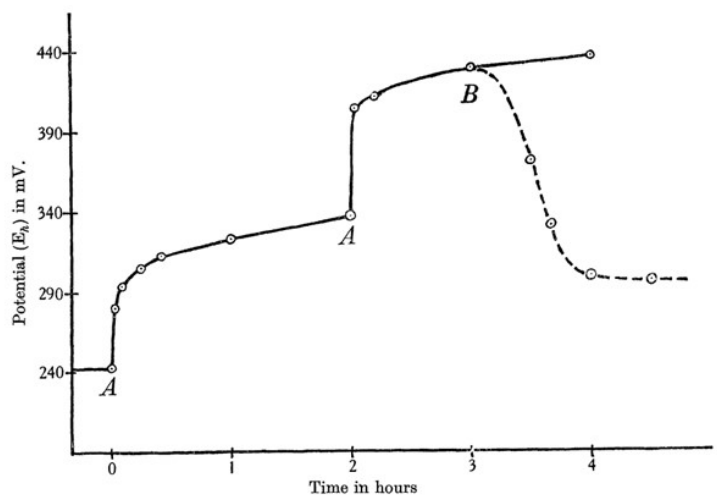

Figure 7. Changes in electric potential (mV) over time in an aqueous mud slurry (Ph 5.59) after bubbling air through it for 30 s at time A and (dotted line) with continuous bubbling of nitrogen through it time B. Figure 1 in Pearsall and Mortimer (1939).

Founding the Freshwater Biological Association

In September 1896, D. J. Scourfield read a paper to Section D of the British Association [for the Advancement of Science] entitled "Wanted, a British Fresh-Water Biological Station." In this paper, Scourfield advocated the establishment of an institution devoted to freshwater biology in Britain like those already in existence in Europe. Although some small research programs in freshwater biology were established in England in the intervening years (Le Cren 1979), a serious movement to establish a scientific laboratory devoted to the study of freshwater biology did not take shape until 1927 following F. E. Fritsch's address to the British Association at Leeds about the need to establish such a laboratory. Fritsch's talk resulted in an ad hoc

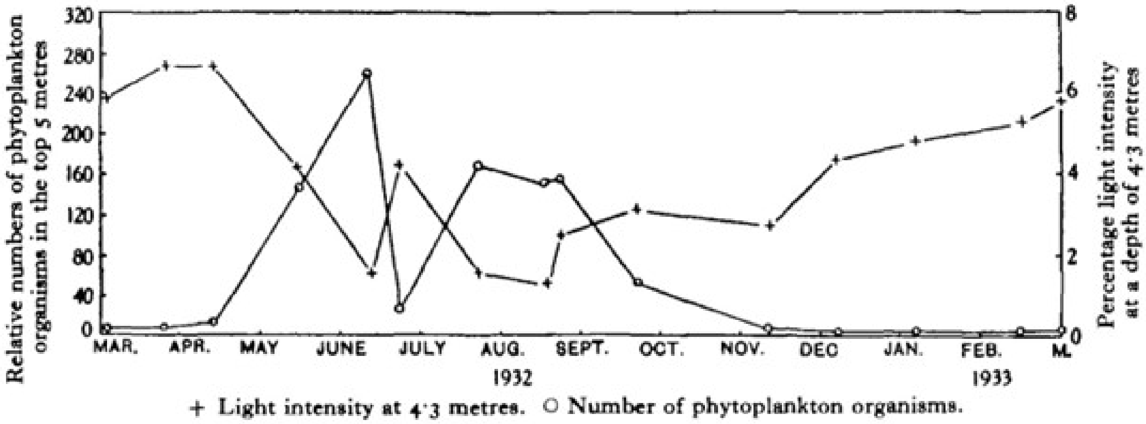

Figure 8. Light intensity at 4.3 m, the limit of aquatic vegetation, and phytoplankton density in the upper 5 m of Lake Windermere from March 1932 to March 1933. Figure 2 in Pearsall and Ulyott (1934).

committee being established in 1928 to explore the feasibility of such a laboratory. Although many other scientists were involved, three men took the lead in making this a reality: F. E. Fritsch (Professor of Botany at Queen Mary University), J. T. Saunders (Lecturer in Zoology at Cambridge), and W. H. Pearsall (Reader in Botany at Leeds).

Because this effort coincided with the onset of the Great Depression (or "Slump" as it was called in Britain), plans to raise money for a new building to house the proposed freshwater research station had to be abandoned. However, in 1929, the Freshwater Biological Association of the British Empire was established (Fogg 1979; Fritsch 1937; Le Cren 1979). Funds to establish a field station were raised by the Association from various individual contributors, angling organizations, the Fishmongers' Company, and the government agency responsible for fisheries research. The obvious location for the new field station was the Lake District because of all the work done there by Pearsall. The Association acquired a few rooms in Wray Castle for its laboratory and the use of its cellars and boat house. Although Wray Castle was conveniently located near two lakes, Esthwaite Water and the north basin of Windermere, this 19th-Century imitation castle was badly in need of repair, and most of it was occupied by the Youth Hostels Association. In short, it was not an ideal place to conduct scientific research.

The laboratory opened in 1931 with a staff of two scientists. At this time, J. T. Saunders was teaching the first university course in "hydrobiology" in Britain at Cambridge, and not surprisingly, the initial scientific staff was recruited from his former or current students. However, because Pearsall, its first Honorary Director (1931-1937), knew the Lake District so well, he provided much of the station's initial scientific direction.

Phillip Ullyott was one of the first staffers hired by the Freshwater Biological Association in 1931. As a follow-up to Peasrsall's earlier studies of factors controlling the distribution of wetland plants in the lakes of the Lake District, Pearsall and Ullyott conducted research on light conditions in Lake Windermere. This study first required developing suitable light measuring equipment (Pearsall and Ullyott 1933) and then deploying it to measure light conditions in situ at different depths (Pearsall and Ullyott 1934). They showed that light penetration into Windermere highly depends on phytoplankton density in the water column (Figure 8). During July and August 1932, blue-green algae reduced the light intensity at the limit of submerged vegetation (4.3 m) by more than 50 % and, since light limits the maximum depth at which submerged vegetation can grow, it is phytoplankton that set this limit in Lake Windermere.

Another early Freshwater Biological Association scientist with whom Pearsall collaborated was Clifford H. Mortimer, who joined the staff in 1935. As noted earlier, Pearsall and Mortimer (1939) published an important joint paper on oxidation-reduction potentials in waterlogged soils and water. Mortimer built on this work and conducted a major study of the sediment-water interface in lakes that demonstrated the importance of oxidation-reduction potential gradients on seasonal patterns in lake water chemistry (Mortimer 1941). According to Google Scholar, Mortimer's "The exchange of dissolved substances between mud and water in lakes" is a classic work in limnology that has been cited over 2000 times.

"The research achievement of the [Freshwater Biological Association] … may fairly be regarded as in large part the triumphant continuation of the work begun by Pearsall and his father, and Pearsall played an active and greatly appreciated role in guiding, encouraging, and inspiring the research workers until the end of his life" (Clapham 1971). Talling (2008) provides an excellent overview of Pearsall's and the Freshwater Biological Association's contributions to the development of the aquatic sciences. From its beginnings, the Freshwater Biological Association's main objective was basic biology research to solve practical problems in managing freshwater resources (Le Cren 1979).

FINAL THOUGHTS

Britain was fortunate that it had two seminal figures so early in the development of wetland science. No work comparable to Arber's *Water Plants* was published in the U.S. until 1976, when the British-born and educated G. E. Hutchinson published his *A Treatise on Limnology. Volume III. Limnological Botany.* Detailed studies of wetland vegetation in multiple bodies of water compared to those of Pearsall's in the Lake District did not occur in the U.S. until the early 1940s, when William T. Penfound and his colleagues studied the vegetation of the Tennessee Valley Authority reservoirs (van der Valk 2022).

Agnes Arber and William Pearsall contributed significantly to wetland science but in very different ways. Arber was not interested in wetlands or wetland plants per se. She was an anatomist, not an ecologist, who believed that she could discover the origin of monocotyledons by studying their anatomy and morphology. She was interested in wetland plants because many families of monocotyledons are solely or predominantly wetland plants, and monocotyledons were believed to have evolved from dicotyledonous wetland ancestors. Although Arber wrote *Water Plants* to explore the evolution of wetland plants, *Water Plants* remained an indispensable reference book for wetland scientists for decades after its publication. Its 65-page annotated bibliography was a treasure trove of information on the biology, ecology, and evolution of wetland plants. It is so extensive that it has its own index.

Agnes Arber was an exceptional writer, and one of the reasons for the longevity of *Water Plants* is that it is easy and fun to read. It is the only work in wetland science I have read solely for pleasure. One of her biographers, Maura Flannery (2005), makes the same point.: "…she is fun to read. She writes extremely well, and extremely clearly. She is learned without being at all dense or obtuse; she is learned in an unselfconscious way that was always rare but is almost unheard of today." If interested in reading her book, *Water Plants* is available online (https://archive.org/details/in.ernet.dli.2015.351383).

Because Arber never held an academic position after leaving University College London, she did not train graduate students who would carry on her legacy, nor did she create any kind of institutional legacy. Arber may have been a one-hit wonder in wetland science, but it was a long-lasting and influential hit. However, I must emphasize that her major scientific contributions and impacts were outside wetland science.

Unlike Agnes Arber, William Pearsall was a successful British academic. His ground-breaking research and publications on the vegetation of English lakes made him the authority on the subject when he was a young man and got him his first permanent academic position. Again, unlike Arber, Pearsall trained graduate students. Two of these, Ramdeo Misra in India and Eville Gorham in Canada and the United States, would become leaders in wetland science outside Britain. However, he was not just a successful academic but an outstanding scientist.

Pearsall collected large quantities of field data, but his uncanny ability to deduce patterns from these data made him an exceptional scientist, as was his ability to propose well-founded explanations of the underlying causes of these patterns. Through his teaching, research, and leadership of the Freshwater Biological Association, Pearsall transformed nascent wetland science from scattered descriptive and taxonomically focused natural history studies into a rigorous and coherent branch of science.

One thing that Arber and Pearsall did have in common was an international perspective. They both paid careful attention to research publications from scientists in continental Europe and North America. By the late 19th and early 20th Centuries, numerous studies had already been published on aquatic systems, especially lakes (Egerton 2014). *Water Plants* is essentially a review of previously published papers. Pearsall was influenced by the work of several American scientists like Raymond Pond (1905) and the water chemistry and light penetration studies of Wisconsin limnologists E. A. Birge and Chancey Juday.

REFERENCES

Arber, A. 1912. Herbals, their Origin and Evolution: A Chapter in the History of Botany, 1470-1670. Cambridge University Press, Cambridge, UK.

Arber, A. 1919a. Obituary: Ethel Sargant. October 28, 1863-January 16, 1918. *The New Phytologist* 18: 120-128.

Arber, A. 1919b. Aquatic angiosperms: the significance of their systematic distribution. *Journal of Botany* 57: 83-86.

Arber, A. 1919c. On heterophylly in water plants. *American Naturalist* 53: 272-278.

Arber, A. 1919d. The vegetative morphology of Pistia and the Lemnaceae. *Proceedings of the Royal Society of London*, Series B. 91: 96-103.

Arber, A. 1920. *Water Plants: A Study of Aquatic Angiosperms.* University Press, Cambridge, Cambridge, UK.

Arber, A. 1925. *Monocotyledons: A Morphological Study.* University Press, Cambridge, Cambridge, UK.

Arber, A. 1934. *The Gramineae: A Study of Cereal, Bamboo, and Grass.* University Press, Cambridge, Cambridge, UK.

Clapham, A.R. 1971. William Harold Pearsall. 1891-1964. *Biographical Memoirs of Fellows of the Royal Society* 17: 511-540.

Egerton, F.N. 2014. History of ecological sciences, Part 50: Formalizing limnology, 1870s to 1920s. *Bulletin of the Ecological Society of America* 95: 130-153.

Flannery, M.C. 2005. Agnes Arber in the 21st Century. *The Systematist* 24: 13-17.

Fogg, G.E. 1979. Freshwater Biological Association 1929-1979: The first fifty years. Freshwater Biological Association, Ambleside, U.K.

Fritsch, F.E. 1937. The early history of the Association up to the date of the opening of the laboratory in 1931. *Report Freshwater Biological Association* 5: 33-41.

Guppy, H.B. 1893. The distribution of aquatic plants and Animals. *Scottish Geographical Magazine* 9: 28-33.

Hutchinson, G.E. 1976. *A Treatise on Limnology. Vol. III. Limnological Botany.* John Wiley & Sons, New York, NY.

Le Cren, E.D. 1979. The first fifty years of the Freshwater Biological Association. *Annual Report of the Freshwater Biological Association* 47: 27-42.

Mortimer, C.H. 1941. The exchange of dissolved substances between mud and water in lakes. *Journal of Ecology* 29: 280-329.

Packer, K. 1997. A laboratory of one's own: the life and works of Agnes Arber, F. R. S. (1879-1960). *Notes and Records of the Royal Society of London* 51: 87–104.

Pearsall, W.H. 1917-1918. The aquatic and marsh vegetation of Esthwaite (1917-1918) Water. *Journal of Ecology* 5: 180-202 and 6: 53-74.

Pearsall, W.H. 1918. On the classification of aquatic plant communities. *Journal of Ecology* 6: 75-83.

Pearsall, W.H. 1920. The aquatic vegetation of the English Lakes. *Journal of Ecology* 8: 163-201.

Pearsall, W.H. 1921. The development of vegetation in the English Lakes, considered in relation to the general evolution of glacial lakes and rock basins. *Proceedings of the Royal Society*, B 92: 259-284.

Pearsall, W.H. 1938a. The soil complex in relation to plant communities. I. Oxidation-reduction potentials in soils. *Journal of Ecology* 26: 180-193.

Pearsall, W.H. 1938b. The soil complex in relation to plant communities. II. Characteristic woodland soils. *Journal of Ecology* 26: 194-209.

Pearsall, W.H. 1938c. The soil complex in relation to plant communities. III. *Moorlands and bogs*. *Journal of Ecology* 26: 298-315.

Pearsall, W.H. and C. H. Mortimer. 1939. Oxidation-reduction potentials in waterlogged soils, natural waters and muds. *Journal of Ecology* 27: 483-501.

Pearsall, W.H. and P. Ullyott. 1933. Light penetration into fresh water: I. A thermionic potentiometer for measuring light intensity with photoelectric cells. *Journal of Experimental Biology* 10: 293–305.

Pearsall, W.H. and P. Ullyott. 1934. Light penetration into fresh water: III. Seasonal variations in the light conditions in Windermere in relation to vegetation. *Journal of Experimental Biology* 11: 89–93

Pond, R.H. 1905. The relation of aquatic plants to the substratum. Contribution to the Biology of the Great Lakes, U.S. Fish Commission of Fish and Fisheries, Washington, DC.

Sargant, E. 1903. A Theory of the origin of monocotyledons, founded on the structure of their seedlings. *Annals of Botany* 17:1-92.

Sargant, E. and A. Arber. 1915. The Comparative morphology of the embryo and seedling in the Gramineae. *Annals of Botany* 29:161-222.

Schmid, R. 2001. Agnes Arber, née Robertson (1879-1960): Fragments of her Life, Including her Place in Biology and in Women's Studies. *Annals of Botany* 88: 1105-1128.

Schenck, H. 1886. *Die Biologie der Wassergewächse.* FR Cohen, Bonn, Germany.

Sculthorpe, C.D. 1967. *The Biology of Aquatic Vascular Plants*. Edward Arnold, London, UK.

Talling, F. J. 2008. The developmental history of inland water science. *Freshwater Review* 1:119-141.

Tansley, A.G. 1911. *Types of British Vegetation.* Central Committee for the Survey and Study of British Vegetation, University Press, Cambridge, UK.

Thomas, H.H. 1960. Agnes Arber, 1879-1960. *Biographical Memoirs of Fellows of the Royal Society* 6:1-11.

van der Valk, A.G. 2017. Antecedent wetland ecologists - German and Austrian in the Ninetieth Century. *Wetland Science and Practice* 34: 112-117.

van der Valk, A.G. 1922. Naturalistic control: W. T. Penfound, T. F. Hall, and A. D. Hess and malaria control in Tennessee Valley Authority reservoirs. *Wetland Science and Practice* 40: 12-18.

West, G. 1906. A comparative study of the dominant phanerogamic and higher cryptogamic flora of aquatic habit, in three lake areas of Scotland. *Proceedings of the Royal Society of Edinburgh* 25: 967-1023.

West, G. 1910. VI.—A further contribution to a comparative study of the dominant phanerogamic and higher cryptogamic flora of aquatic habit in Scottish lakes. *Proceedings of the Royal Society of Edinburgh* 30: 65-182.